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ST. GEORGES BAY ECOSYSTEM PROJECT (GBEP): RESEARCH REPORT II: DIETS AND FEEDING

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St. Georges Bay Ecosystem Project (GBEP): Research Report II: Diets and Feeding

By

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Abstract:

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The St.Georges Bay Ecosystem Project Research Report II is a survey of diet studies of marine species of St. Georges Bay, located along Nova Scotia's Northumberland Strait, in the Southern Gulf of St. Lawrence. Integrated into this body of knowledge is data collected from other North Atlantic sites, including the Northern Gulf of St. Lawrence, Bay of Fundy and New England waters. The report inventories the feeding studies of pelagic, benthic, and coastal estuarine fish species of St. Georges Bay as well as benthic invertebrates, marine mammals and seabirds.

Résumé:

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Le rapport II sur le projet de recherche touchant à l'écosystème de la baie St. Georges consiste en une étude de l'alimentation des espèces marines de la baie St. Georges situées le long du détroit de Northumberland jouxtant la Nouvelle-Écosse, dans le sud du golfe du Saint-Laurent. Sont incorporées à cette somme de connaissances des données recueillies d'autres sites de l'Atlantique Nord, y compris le nord du golfe du Saint-Laurent, la baie de Fundy et les eaux baignant la Nouvelle-Angleterre. Le rapport inventorie des études sur l'alimentation des espèces de poissons pélagiques, benthiques et côtiers estuariens de la baie St. Georges ainsi que des espèces d'invertébrés benthiques, de mammifères marins et d'oiseaux de mer.

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Introduction

This report is an exploration of knowledge pertaining to predation among marine species known, or suspected to occur in St. Georges Bay, as well as avian predators which play an important role in this ecosystem. It will also serve as an opportunity to identify areas which are well understood and others requiring significant study effort.

The report is a survey of diet studies for organisms within St. Georges Bay. As the body of knowledge published that applies directly to the diets of species within St. Georges Bay is small, this report also presents what is known about diet of local species as they exist in adjacent ecosystems.

St. Georges Bay is a shallow embayment, roughly 900 km^2, with a maximum depth of 40 m, and average depth of approximately 24 m (Hargrave et al., 1985). It opens to the north, into the Northumberland Strait, within the southeastern portion of the Gulf of St. Lawrence. The oceanography of the bay is well documented by Petrie and Drinkwater (1978), and a comprehensive review of the biology and physical characteristics of the study area are presented in Cameron et al. (2000).

Diet Studies

A common method of examining diet requires that the materials found in the stomachs of individuals are examined and quantified. Other approaches include the examination of regurgitated material, which some species will readily avail; analyzing regurgitated pellets or faeces which contain bones used for identification; and observation of feeding habits. All but the first method are more suited to terrestrial predators, and the latter may be restricted by the interference with normal feeding behavior by the observer.

Results of examinations of stomach contents are expressed in a variety modes, chiefly the following:

- *percent occurrence*; percentage of stomachs in which a prey group is found
- *percent weight* of stomach contents that is contributed by a particular prey species
- *percent volume* of stomach contents contributed by a prey group
- *percent frequency* which is the proportion of all prey occurrences that a prey group represents.

Where possible, percent weight data was presented in this report, thus selection of data was partially biased towards data presented in this mode.

Both field and laboratory studies are included in the following discussion. Several caveats must be borne in mind in interpreting stomach contents and laboratory food preference experiments.

Field Studies

- Food items differ in their digestion time, calorific value, and residence times, and this causes an underestimation of highly digestible (i.e., soft bodied prey) and possibly energy rich food (Hudon and Lamarche, 1989).
- In the field the density of a prey item could exceed a certain saturation level and, therefore, appear to rank low in preference, although it is actually highly selected (Pyke et. al., 1977).
- In field studies, the immediate accessibility of a prey type as well as its detectability can be important for food selection and could partly explain why some highly abundant prey categories may seem to be "avoided" (Wieczorek and Hooper, 1995). That is, they may not be detected or accessible.

Laboratory Experiments

- Food selectivity may be influenced by variations in internal motivational state, overall activity/starvation level, past experience and [for decapods] its moulting state (Wieczorek and Hooper, 1995).
- In laboratories, escape may be impossible for mobile prey as they are confined within a tank (Evans and Mann, 1977; Elner and Jamieson, 1979), thus overestimating the consumption rates for a predator of a prey item.
- Provision of the full spectrum of food resources for a predator is not possible, and so the effects of combinations of prey items is not possible to evaluate at this time.

CONSIDERATIONS IN APPLICATION OF DIET STUDIES

The biological systems within which diet studies are conducted are complex, and because species populations are in continual flux, identification of a reference baseline for any activity requires considerable care. Observations of diet of individuals at any one time may not be considered representative of long-term status, but stable food web linkages may be demonstrated by numerous sampling events. One must then consider whether variations in observed diets are the result of different distributions of prey abundance, local differences in predator preferences or lack of preference. Distribution of predator and prey species vary with a variety of significant diurnal, seasonal and life cycles. This results in changes in relative predator/prey densities, which may alter predator diet. Because of this, discussion of feeding habits may require qualification in terms of sampling time, season, depth, location, distance from shore, and mode of capture.

Because distribution of prey groups may vary geographically according to differing conditions, care must be taken in applying information from other locations. The information presented in this report provides detail on feeding from areas adjacent that are potentially representative, and others with outstanding differences from the bay.

Analysis of consistency of diets of predators from different conditions is instructive in terms of understanding the strategies a predator may utilize in feeding, and allows assessment of feeding predictability. The following discussion is presented in

order to give the reader a very general understanding of the variability in conditions that influence species distribution within and outside of the Gulf of St. Lawrence. Figure 1 provides location of areas discussed.

The physical features of the Gulf of St. Lawrence result in freshwater influence in the west; depth with its resultant low temperature in the center and along the northern shore; and the lack of coastal context in the east. These are all features that distinguish these regions from the area south of the Laurentian Channel. Comparison of the biological communities within these areas can be found in de Lafontaine et al. (1991).

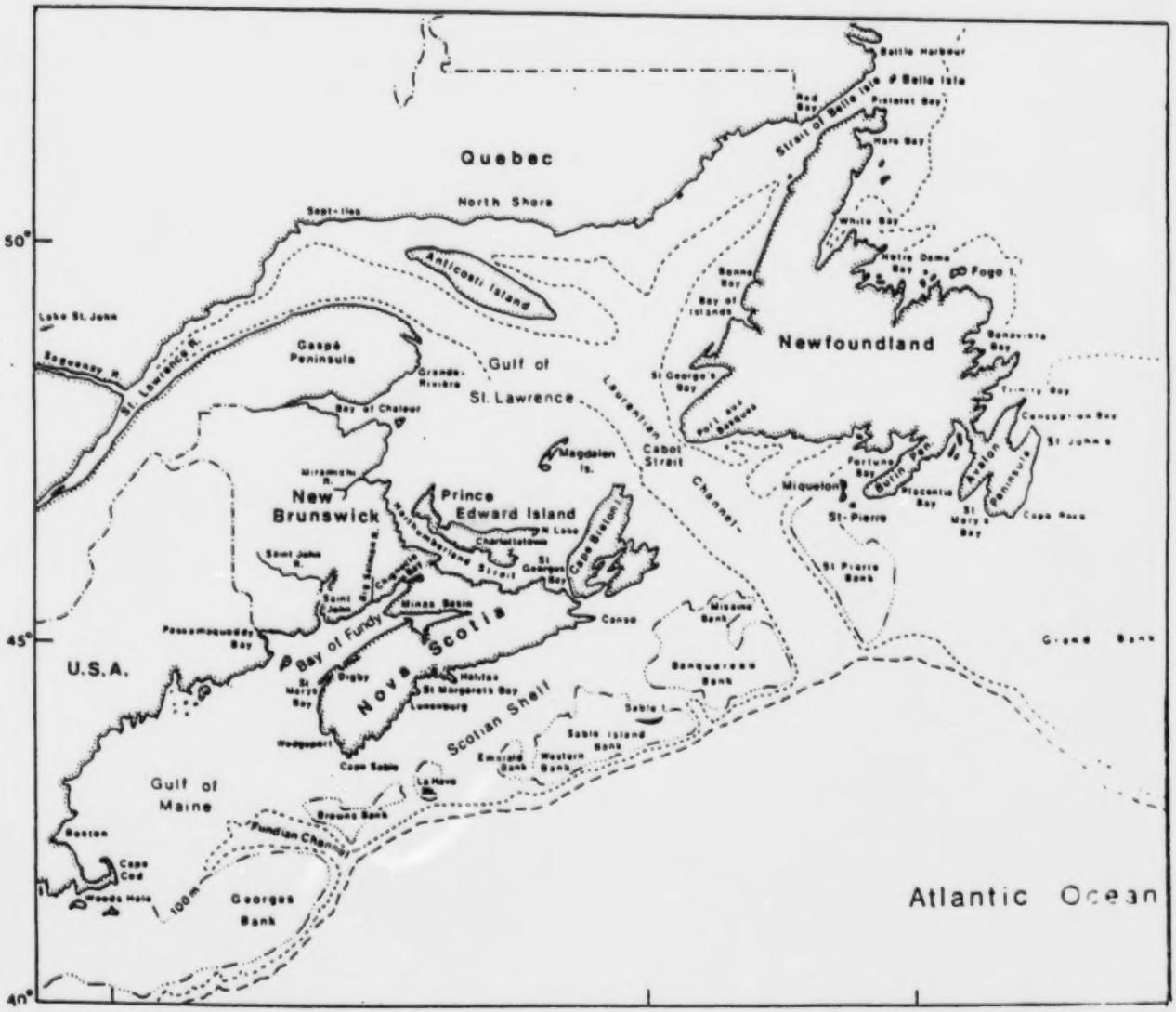

Figure 1: Canadian Atlantic area showing major fishing banks (Scott and Scott, 1988).

The southern Gulf is described in terms of two regions by Dunbar et al. (1980). The Magdalen Shallows, which are characterized by water depths over 60 m, lie to the north of an area including the Prince Edward Island and the Northumberland Strait, and is delineated from this area by an average summer isotherm of 18 °C. The southern water mass is less than 60 m deep, has a greater coastal influence, an abundance of beaches, low shoreline profile, and warm salt Virginian marine climate (Dunbar et al, 1980).

The composition of the marine fauna of the southern Gulf is a balance of northern species with cold water subarctic affinities and southern species. Thus, their combined range is from the subarctic to Mexico (Dunbar et al., 1980). This balance changes in proportion as one travels north or south. The southern Gulf represents the northern limit of a discontinuous distribution of some warm water fauna found along the Atlantic seaboard. Examples of southerly species are the American oyster, and American lobster, the great blue heron, bluefin tuna, blue shark, ocean sunfish and American eel. The interaction of the individual species of these groups within the unique oceanographic setting is not duplicated in adjacent waters (Bousefield and Laubitz, 1972) cited in Dunbar et al. (1980).

Because there are no significant physical oceanographic differences between the southwestern and southeastern portions of the Gulf within which the study area is located, studies from the southwest would be expected to reflect conditions in the southeast. There are observed variations in species distribution (Kenchington, 1980) which must be considered in comparison. Furthermore, conditions within St. Georges Bay are unique within the southeastern Gulf, as it is a small semi-enclosed, shallow water body (Hargrave et al., 1985).

There is a wealth of diet information published on Atlantic locations. Those that pertain to the coastal shelf, such as the Scotian Shelf, Georges Bank, Gulf of Maine and Newfoundland have been included in order to provide some terms of reference for St. Georges Bay. Atlantic sites differ significantly from Gulf sites because of the lack of ice cover and warmer waters in the winter, as well as higher nutrient concentrations (de Lafontaine et al., 1991) and productivity (Hargrave et al., 1985). However, these sites are host to many of the Gulf of St. Lawrence species during annual migrations, so they could in fact be samplings of the same populations that visit St. Georges Bay.

Diet information from these sites is also useful for the purpose of examining the degree of uniformity or variation of diets of particular species over geographical area. The Cape Cod and southwest Gulf regions are areas which have many of the same features; high summer and low winter temperature, low tidal amplitude, high proportion of sandy shoreline and are separated by a zone markedly dissimilar (Dunbar et al, 1980). The implication of this is that diet studies from the Cape Cod area may be as, or more appropriate to the southern Gulf than other more proximal areas. Consideration of climate alone would cause one to question this, however, the value of application of information from other regions will only be understood when there is sufficient information available from St. Georges Bay to compare with.

The data presented in this paper were collected from a wide range of sources. Methods of describing and reporting diet specifics vary according to author. Uniformity in presentation in some cases required modification and interpretation of data from the form presented by the author. In this process, priority was given to maintenance of the integrity of the data. Within data tables, - denotes a value of zero for a prey category, and · denotes that the prey category was not reported by the author.

The fish predator species discussed were taken from Cameron et al. (2000) unless otherwise stated, and are presented with scientific names in Appendix 1. Those fish, which are suspected to be less common or believed to be poorly represented by trawl sampling, are identified. Scientific names of additional species discussed are presented in Appendix 2. Biomass estimates of some species for St. Georges Bay are presented in Appendix 3 (Kenchington et al., 1980).

It should also be emphasized that the time frame of this report allowed for a limited survey of available information. It is possible that relevant information has not been reported. In addition, although there may be little direct information on feeding habits of species within St. Georges Bay, this is not to say that the feeding of some species is not well understood. There is a large volume of work devoted to some of these species worldwide, and extensive experimental work in feeding preference which could not be reported within the time frame available.

Where possible, some taxonomic detail was included for the reader's benefit. Because of the large number of organisms discussed it was not possible to provide classification for all. In lieu of this, the reader may refer to Shih et al. (1971), Gosner (1978), Hobson and Banse (1981), Gardner and Szabo (1982), Bernard (1983), Kathman et al. (1986) and Squires (1990).

1. Pelagic Production and Feeding

This section includes discussion of production and feeding of the plankton components of the pelagic system as well as diet of pelagic fish and invertebrate species.

1.a The Plankton Community

PHYTOPLANKTON

The plankton community is one aspect of the St. Georges Bay ecosystem which has been systematically studied in terms of abundance and potential interactions of its various components.

The phytoplankton population of St. Georges Bay is characterized as having a short bloom in the spring with low biomass and low variability relative to other areas within the Gulf of St. Lawrence (de Lafontaine et al., 1991). The central Gulf of St. Lawrence tends to have higher concentrations of chlorophyll a, indicating greater phytoplankton activity, relative to near-shore environments (Lambert et al., 1982a).

Phytoplankton production rates (Table 1) are half those of shelf regions such as the Grand Banks (Hargrave et al., 1985). The key limiting factor in the productivity is believed to be the lack of nutrient contribution from upwelling of a nutrient-rich deep water layer absent in the St. Georges Bay (de Lafontaine, 1991).

Phytoplankton abundance was observed by Hargrave et al. (1985) as prominent peaks in chlorophyll a values in June and October (40 mg/m^2) in St. Georges Bay. Other periods of increased values provided evidence of blooms in April and as early as January. Phytoplankton production was observed near the surface, in the upper 10 m, and maximum chlorophyll a concentrations were found below 10 m (Hargrave et al., 1985).

Phytoplankton abundance is a function of productivity, intensity of predation, and rates of sedimentation. These processes are discussed in Hargrave et al. (1985) and are significant contributions to the transfer of energy to the pelagic and benthic ecosystems. Production has been observed to be low in early summer and is thought to be limited by

Table 1: Productivity of phytoplankton populations of St. Georges Bay, the Bras d'Or Lakes and the Grand Banks (mg C/m^2/day) in 1977, from Hargrave et al. (1985).

	St. Georges Bay	Bras d'Or Lakes	Grand Banks
May	153	123	1710
June	223	390	606
July	290	313	280
August	490	427	238
September	517	247	299
October	403	450	-

consumption of utilizable nitrogen compounds by the April bloom (Hargrave et al., 1985). Average production levels showed clearly increasing peaks on an approximately monthly basis from June (200 mg C/m^2/day) to September (700 mg C/m^2/day). Production rates increase throughout the summer as nutrients become available, but chlorophyll a concentrations do not increase. This is the result of grazing pressure imposed as the zooplankton population increases.

During the early spring and late fall, reduced grazing pressure allows phytoplankton production to exceed the carrying capacity of its environment. The result is an increased rate of sedimentation of organic carbon and nitrogen into the water column. This contribution is believed to be quickly assimilated. Hargrave et al. (1985) found that the dry weight of organic carbon of bottom sediment never exceeded 2 % during peak sedimentation, and declined quickly afterwards. Rates of phytoplankton production and compound sedimentation in St. Georges Bay are presented in Table 2.

Table 2: Monthly phytoplankton production (g C/m^2), rates of sedimentation of organic carbon (g C/m^2) and organic nitrogen (g N/m^2) at two stations in St. Georges Bay, 1977 (Hargrave et al., 1985).

	Station 1			Station 2		
	Phytoplankton production	Carbon sedimentation	Nitrogen sedimentation	Phytoplankton production	Carbon sedimentation	Nitrogen sedimentation
May	3.7	5.0	0.7	3.2	3.8	0.5
June	4.8	1.1	0.2	5.1	1.5	0.2
July	9.9	1.1	0.2	7.4	1.6	0.2
August	14.9	1.9	0.3	12.7	1.1	0.2
September	15.1	6.5	0.9	14.0	3.9	0.6
October	12.5	3.8	0.5	11.1	3.8	0.5
Total	60.5	19.4	2.8	53.5	15.7	2.2

ZOOPLANKTON

Average zooplankton biomass was found to peak at higher than 80 mg wet weight/m^3 in July, decreasing and then forming a second peak in August, falling to less than 20 mg/m^3 in late September, and returning to high levels (92 mg/m^3) in November (Lambert., 1980).

The first peak in the early summer was placed predominantly in the surface layer, chiefly composed of mackerel eggs (*Scomber scombrus).* Small copepods were dominant throughout the summer, and larger calanoid copepods thrived in the fall.

A large proportion of the zooplankton biomass (75%) is contributed by copepods, which is duly reflected in the prominence within diets of zooplankton predators (Ware, 1980). Relative abundance of copepod species are presented in Table 3. Other

Table 3: Abundance of copepod species in St. Georges Bay, Lambert (1980).

High	Low	Rare
Calanus finmarchicus	*Acartia hudsonia*	*Aetideus sp.* (benthic)
Centropages hamatus	*Acartia longiremis*	*Bradyidius similis*
Temora longicornis	*Anomalocera ovalus*	*Calanus hyperboreus*
Tortanus discaudataus	*Centropages typicus*	*Eurytemora herdmani*
	Labidocera aestiva	*Harpacticus chelifer*
	Oithona similis	*Metridia longs*
		Metridis lucens
		Scolecithricella minor

components of the zooplankton community include cirripedes and cladocerans, being numerically significant in the spring, and summer/fall, respectively, as well as krill, mysids, larvae of bivalves and echinoderms, and decapods, arrow worms, and cnidarian medusae (Lambert, 1980).

Comparison of these abundances with other regional marine populations reveals that *Acarti* and *Calanus* are more prevalent in Gulf of Maine, *Pseudocalanus* and *Oithona* are more abundant in St. Margarets Bay, and *Temora* and *Tortanus* are less abundant in the Atlantic Ocean than in St. Georges Bay.

A distinct seasonal succession of zooplankton species in four assemblages was observed in the St. Georges Bay by Lambert (1980). These are listed below beginning with most abundant for each time period.

May 30 to July 30	*Temora -Calanus-Tortanus*
August 1 to September 30	*Temora-Centropages-Tortanus*
October 1 to November 1	*Tortanus-Centropages-Temora*
December 1 to December 9	*Tortanus-Calanus*

Hargrave et al. (1985) established that there is a trend towards increased body size with decreased water temperature, thus large zooplankton, *Tortanus*, 2.15 mm in length, and *Calanus*, 3.25 mm, were dominant in the spring and fall, while small zooplankton, *Temora* and *Centropages* (1.25 and 1.3mm respectively), were dominant during the summer months.

Zooplankton biomass declines abruptly in July when larval fish increase in numbers (Hargrave et al., 1985). Predation pressure upon zooplankton remains relatively constant through the summer, as various species of fish larvae successively develop and prey upon the population. It is this predatory pressure upon the herbivorous zooplankton that allows primary production to generate increasing biomass, resulting in the fall phytoplankton bloom (Hargrave et al., 1985).

Although faecal pellets are considered a major contributor to benthic organic matter, Hargrave et al. (1985) observed low levels of faecal deposition in St. Georges

Bay. This could be attributed to breakdown and consumption of the pellets within the euphotic zone before reaching the sediment.

Other facets of the food web require study as net size and focus of previous studies have neglected details of other potential contributors such as smaller zooplankton and jellyfish (de Lafontaine et al., 1991).

ICHTHYOPLANKTON

Within the Gulf of St. Lawrence, the southern Gulf, including St. Georges Bay is distinguished as an important 'nursery' for many resident and migratory fish species (de Lafontaine et al., 1991). Thus the prevalence of larval stages of fish is a significant feature of this ecosystem. The conditions of the bay; a regular pattern of summer warming (Ware, 1977), and low flushing rate (Petrie and Drinkwater, 1978), provide an early, relatively stable environment within the gulf for successful spawning.

Migratory, commercially important species dominate the pelagic fish biomass of the southern Gulf (Hargrave et al., 1985). A number of pelagic fish such as mackerel, herring, and capelin; mesopelagic fish including cod, hake, and fourbeard rockling, and benthic fish (plaice and flounder) spawn in St. Georges Bay (Lambert and Ware, 1984). Additionally, many benthic invertebrates, particularly American lobster and rock crab contribute larval stages to the pelagic ecosystem (Hargrave et al., 1985). The larvae chiefly feed on zooplankton, as do many of the adults, but feeding in adults is greatest before spawning for several fish species as will be demonstrated throughout this report, and then declines drastically during the time that larval and juvenile fish are feeding intensively.

Hargrave et al. (1985) present production rates for components of the plankton community (Table 4). Larval mackerel productivity values are presented as examples only and are not intended to represent other species of ichthyoplankton. American lobster is also presented for comparison.

Table 4: Comparison of phytoplankton, zooplankton and larval mackerel and lobster production over 6 months, 1975 and 1978 in St. Georges Bay (mg C/m^2), Hargrave et al. (1985).

Month	Phytoplankton	Zooplankton 125-1028 µm	Mackerel larvae	Lobster larvae
May	3,500	500 (15)	-	-
June	5,000	600 (12)	0.4	0.0004
July	8,700	1,100 (13)	15.6	0.2357
Aug.	13,800	900 (07)	0.8	0.2490
Sept.	14,600	900 (06)	-	0.0133
Oct.	11,800	1,000 (08)	-	-

Numbers in parentheses are percentages of phytoplankton production.

The variation among fish species in terms of predatory impact is not as great as the variation among developmental stages. The chief factors contributing to this are gape (size of mouth) and body size (Hargrave et al., 1985). Zooplankton above specific size limits will be not be preyed upon by larval fish that can not yet ingest them. Thus it can be productive to discuss predation in terms of predators within size groups rather than species.

It has been demonstrated that the timing of spawning, and nature of spawning mass enables an efficient utilization of the available zooplankton biomass. Also, a clear succession of spawning peaks in the bay by different species was reported, which would allow reduced interspecific competition for food resources (Lambert, 1980). Cod and plaice spawn in May, June spawning includes fourbeard rockling and yellowtail flounder, and white hake and cunner spawn in July, the latter constituting up to 50 % of the larval fish biomass in the bay (Hargrave et al., 1985).

Spawning waves within a species were found to be timed so that the increased mouth size in earlier hatchings allowed for a broader feeding range and therefore a reduction in prey competition with newly hatched larvae (Lambert and Ware, 1984). As well, it was found that the feeding range differed between species, which would reduce competition between the species.

Atlantic mackerel larvae

Ware and Lambert (1985) have published data on larval mackerel diet collected within St. Georges Bay. Diet was found to reflect abundance and distribution of prey. Copepods contributed the largest proportion to larval mackerel diet, particularly *Evadne* sp., a near-surface zooplankton. Near-surface fish larvae, including mackerel, become part of the diet with increased size, but the incidence of cannibalism was noted to disappear at the time when young fish initiate schooling behavior. Other fish larvae consumed were white hake and fourbeard rockling. The selection of larger prey within the larval mackerel prey range was also observed. Patterns of spawning, largely defined by temperature conditions, were found to take advantage of the period of abundance of appropriately sized planktonic prey. Ware and Lambert (1985) also observed greater growth rates at times when average size of plankton prey was larger.

Feeding of mackerel larvae on the Scotian Bank was examined by Fortier and Villeneuve (1996). Resulting data, presented in Table 5, demonstrates the change in feeding with size. The smallest larvae consume chiefly copepod nauplii, then with increased size, copepods and fish larvae become progressively more abundant prey. Feeding on copepods was observed to be density dependant, but feeding on fish larvae was density independent. Fish larvae as prey were scarce relative to copepods, and the selection of larval prey was believed to be motivated by the increased gains in volume, as they did not represent higher caloric value per volume.

Of fish larvae consumed, 66 % were mackerel, 18 % were yellowtail flounder, 12 % were silver hake and 4 % were redfish. Larvae consumed were exclusively new hatchlings, estimated to constitute from 7 % to 57 % of the standing crop of hatchlings.

Table 5: Percent composition of diet, by length class for larval Atlantic mackerel from the Scotian Shelf, July 1991 (Fortier and Villeneuve, 1996).

	Length class (mm)					
Prey taxa	<5	5-<6	6-<7	7-<8	8-<9	≥9
Copepod eggs	<1	<1	<1	18	46	37
Copepod nauplii	89	63	56	23	2	8
Copepods *	5	21	30	41	34	34
Appendicularians	4	7	4	5	2	1
Fish larvae	2	9	9	12	14	16
Others **	<1	<1	<1	1	2	4
Total prey	742	1655	2913	1350	570	227
Total mackerel larvae	172	444	523	322	144	62

* Copepodites and adult copepods

** Include euphausiids, chaetognaths, gastropods, phytoplankton cells, cladocerans, amphipods, krill nauplii, and crab larvae in order of decreasing frequency.

The incidence of cannibalism was believed to be a reflection of the relative abundance of mackerel larvae (Fortier and Villeneuve, 1996).

Atlantic cod larvae

Winter feeding of larval cod was examined by McLaren and Avendano (1995) on the western Bank of the Scotian Shelf (Table 6). Copepod consumption was correlated to field densities, larval size, and time of day. Smaller larvae ate nauplii of *Pseudocalanus* and *Centropages typicus*, larger larvae consumed larger prey, mostly *Pseudocalanus* copepodids. There was clear correlation of distribution of these species and of cod larvae. As well, predator selection of these species was apparent as there were other potential prey species present in abundance. Prey density was found to be significant to first-feeding larvae, as they are less mobile in the water column, however, for post-first feeding cod larvae, prey density was not important.

Table 6: Occurrence of prey items in 177 larval cod stomachs, Western Bank of the Scotian Shelf, late fall, 1992, from McLaren and Avendano (1995).

	Stomachs containing prey	Number of prey occurrences
Pseudocalanus spp. nauplii	162	965
Centropages typicus nauplii	150	694
Pseudocalanus spp. copepodids	93	323
Limacina sp. (<0.25 mm)	31	120
Oithona similis copepodids	23	27
Other nauplii	17	24
Other small copepodids	6	1
Centropages typicus copepodids	3	3
Paracalanus parvus copepodids	2	2

Atlantic herring larvae

Lambert et al. (1982) report a linear relation between larval herring length in St. Georges Bay and mean zooplankton prey size. In laboratory studies, Checkley (1982) observed that in addition to selecting the largest ingestible prey, larval herring selected prey according to species. From natural assemblages, herring larvae of all sizes preferentially consumed copepod nauplii and copepodites. *Pseudocalanus* sp. and *Oithona* sp. copepodites were selected by smaller and larger larvae, respectively.

Damkaer and Au (1974) describe the diet of herring larvae on Georges Bank (Table 7). Stomachs tended to contain just one food type, the most common being copepod eggs and bivalve larvae of *Mytilis, Ostrea, Venus,* and *Mya* sp. Size of prey ranged from 6 to 16 mm and was correlated with predator size. Only the largest larvae (10-16 mm) consumed adult copepods. Larger larvae also continued to consume small prey and therefore fed from a greater size range.

Table 7: Numbers of Atlantic herring larvae stomachs containing prey groups (total number of stomachs examined = 166), northeastern Georges Bank, autumn 1970, from Damkaer and Au (1974).

Prey group	Number of stomachs containing
Copepod eggs	103
Copepod nauplii	9
Juvenile copepods	16
Adult *Pseudocalanus*	1
Adult *Paracalanus*	6
Adult *Oithona*	6
Bivalve larvae	82

Noskov et al. (1978) found Georges Bank herring larvae to begin feeding at 5 mm in length and consume eggs and nauplii of copepods, and also molluscs in the size range of 1.0-3.6 mm. Eight to thirteen mm long larvae fed on 1.5-4.0 mm copepodite stages of copepods, and those larger fed upon 1.2 –2.8 mm older copepodites.

Cohen and Lough (1983) report *Pseudocalanus* sp. *P. parvus, C. typicus, C. hamatus, Oithona* sp. and *C. finmarchicus* as chief prey species of herring larvae, in order of proportion contributed. Feeding shifted from smaller nauplii and copepodites to adult stages and larger species with increased larval size.

Time did not allow for a thorough investigation of larval feeding habits of fish of St. Georges Bay. Table 8 presents general diet components for first-feeding and post first-feeding fish of the Scotian Shelf compiled by Mousseau et al. (1998). Larval fish can consume 30 to 40 % of their body weight per day in natural conditions (Hunter, 1980 in Hargrave et al., 1985). This value rapidly decreases with size, although volume eaten may not, as body size is increased. This predation pressure upon the ecosystem is

considerable, and it is believed that food availability to larvae largely defines year class success (Noskov et al., 1978).

Mousseau et al. (1998) discuss the transfer of energy through the food web, and challenge the traditional understanding that the success of year class is critically dependant on the herbivorous food chain, that is, productivity of the spring bloom of large phytoplankton (> 5μm) and subsequent productivity of calanoid copepods. Their analysis of larval feeding on the Scotian Shelf suggests a second trophic pathway is utilized by fish which feed also on smaller zooplankton such as cladocerans and appendicularians, which in turn, utilize the microbial food web and small phytoplankton (< 5μm), abundant after the spring bloom. The fish believed to utilize this alternate trophic pathway are sand lance, Atlantic mackerel, red hake, cunner, windowpane, yellowtail and witch flounder, which are illustrated as having a feeding pattern distinct from the other species listed in Table 8.

Investigations of western Gulf of St. Lawrence plankton populations by Tamigneaux et al. (1997) also suggest the existence of a second pathway utilized during the summer, which reflects seasonal variation in prey abundance.

Table 8: Major prey items (≥ 8% of diet) of first feeding (1) and post-first feeding (2) fish larvae sampled on the Scotian Shelf. Data from various sources, presented in Mousseau et al. (1998).

	Copepods						
	Nauplii	Calanoid	Cyclopoid	Pteropods	Cladocerans	Appendic-ularians	Others
Pollock	2	2	-	1,2	-	-	-
Sculpins	1	2	-	-	-	-	-
Atlantic cod	1,2	2	-	1,2	-	-	-
Redfish	2	2	2	-	-	-	-
Silver hake	1	2	-	-	-	-	-
Atlantic herring	1	2	2	-	-	-	-
Fourbeard rockling	1,2	-	-	-	-	-	-
Sand lance	1,2	2	2	-	-	2	Tintinnids (1)
Atlantic mackerel	1	-	-	-	2	2	Fish larvae (1,2)
Red hake	1,2	-	-	-	2	2	-
Cunner	1	2	-	-	2	-	-
Windowpane	1	2	2	-	1	1	-
Yellowtail flounder	-	1,2	-	-	-	1,2	-
Witch flounder	-	1	-	-	-	1,2	

1.b Feeding of Pelagic Fish

CLUPEIDAE

Atlantic Herring · *Clupea harengus L.*

The herring population in the Gulf of St. Lawrence is noted as having experienced significant fluctuations within the last few decades. A fishery was developed in the 1960's to utilize the then abundant herring resource, but by the early 1970's there was significant decline in numbers. Concern over the decline of the herring fishery promoted some investigation of herring biology in the Gulf. Among other factors, food availability for larval stages is thought to be a significant player in populations prone to such fluctuation in numbers (Messieh et al., 1979).

The herring of the Gulf of St. Lawrence are a distinct stock which overwinters in southwest Newfoundland and travels in the summer to spawn in rich feeding grounds of the southern Gulf (Scott and Scott, 1988). Winters and Becket (1978) noted that the intensive fishery in the 1970's at locations throughout the Gulf and southern Newfoundland was actually subjecting this one migrating stock to an exploitation rate greater than 50 % and nearly year-round harvest pressure.

Messieh et al. (1979) found herring throughout the Gulf, Maine, eastern Nova Scotia and the Bay of Fundy to depend largely on holoplanktonic organisms. Meroplankton, the egg and larval stages of larger organisms, were less significant as a food source (Table 9). Epibenthic species, occurring occasionally in the herring diet

Table 9: Percent occurrence of prey groups for 1120 mackerel stomachs in the Gulf of St. Lawrence, eastern Nova Scotia, Bay of Fundy and the Gulf of Maine 1970 – 1973. Adapted from Figure 5 presented in Messieh et al. (1979).

Prey group	% occurrence
Calanoids	47
Krill	35
Amphipods	12
Fish Eggs	11
Harpacticoids	7
Medusae	5
Arrow worms	3.5
Decapod larvae	3
Invertebrate eggs	2
Pteropods	1
Cyclopoids	1
Ctenophores	1
Fish larvae	1

Values less than 1 % not tabulated.

are thought to be utilized as an alternate food source. Calanoid copepods contributed to the diet of the greatest number of herring, with krill, amphipods and fish eggs found in fewer stomachs.

Bowman et al. (1976) found considerable variation in herring diet among Atlantic sites (Table 10). Gulf of Maine and western Nova Scotia herring diets were composed of 99.6 % and 86 % krill, respectively. Herring at other locations fed considerably less on crustaceans (southern New England, 27.7 % and Georges Bank, 54.4%). Herring at the latter sites fed more heavily on arrow worms (57.4 % and 28.6 %, respectively). In southern New England, krill consumption was replaced by feeding on cumaceans and copepods.

Table 10: Percent weight of prey items found in stomachs of Atlantic herring, collected from the Northwest Atlantic during 1969-1972, Bowman et al. (1976).

	S. New England	Georges Bank	Gulf of Maine	W. Nova Scotia
Hydrozoa	-	**0.1**	-	-
Crustaceans	**27.7**	**54.4**	**99.8**	**86**
Amphipods	0.1	0.1	0.1	-
Caridean shrimp	1.6	-	-	-
Cumaceans	6.2	-	-	-
Krill	0.3	51.2	99.6	86
Copepods	16.5	1.9	-	-
Unidentified	3.0	1.2	0.1	-
Molluscs	**6.6**	**2.5**	-	**0.3**
Pteropods	6.6	2.5	-	0.3
Arrow worms	**57.4**	**28.6**	-	-
Sea squirts	**0.1**	**0.1**	-	-
Fish	**1.1**	-	-	-
Sand lance	0.6	-	-	-
Unidentified	0.5	-	-	-
Animal remains	7.1	14.3	0.2	13.7
# Stomachs	198	98	28	14
Percent empty	15.2	21.4	25	7.1

Scott and Scott (1988) suggest that herring diet is initially heavily dependent on small phytoplankton, but moves to larger prey as they grow. Krill becomes more abundant in adult herring diet, but adults continue to feed on a variety of organisms including those discussed above, as well as fish such as sand lance, silversides, herring and capelin.

Diet of juvenile herring from the coast of Maine consists chiefly of copepods, but this was found to vary seasonally and locally, thus juveniles appear to be opportunistic feeders (Anonymous, 1971).

Messiah et al. (1979) report herring feeding patterns of the Gulf of St. Lawrence as being most intense during July to September, but also in March and May. The proportion of empty stomachs decreased, and the proportion of fish as prey increased in October to November. They found this pattern reflected off eastern Nova Scotia, but in the Bay of Fundy and Gulf of Maine, feeding appeared to peak in the spring and fall with low feeding intensity during the summer. Crawford (1980) reported little feeding during July, August and September in the Pictou County area. Thus a considerable amount of variability is observed regionally.

Frequency of the largest group of prey species, calanoid copepods, were examined in herring diet of Baie des Chaleur, western Gulf of St. Lawrence, by Messieh et al. (1979), presented in Table 11. Here, *C. hyperboreus, C. finmarchicus*, and *T. longicornis* were prey consumed in equal proportions over the whole year, however, consumption of each species varied throughout the year. There is a distinct transition from a more diverse diet in May and June to a diet restricted to fewer prey in the summer and fall. Among the calanoid copepods, *C. hyperboreus* was the dominant prey in May and June and *C. finmarchicus*, and *T. longicornis* were heavily consumed in May and August.

Meganyctiphanes norvegica was the most frequent krill consumed, despite a greater availability of another krill species, *Thysanoessa raschii*. Thus there appears to be a certain amount of selectivity in predation.

Table 11: Percent occurrence of most prevalent zooplankton in herring stomach samples from Baie des Chaleurs during 1970-1973 from commercial catches, number of stomachs = 701, Messieh et al. (1979).

	May	June	July	August	September	October
Calanoids						
C. hyperboreus	24	38	-	-	-	10
C. finmarchicus	20	8	-	24	-	12
Temora longicornis	20	8	-	56	-	-
Metridia longa	8	16	-	-	-	-
Krill						
Meganyctiphanes norvegica	36	15	100	84	-	16
Thysanoessa raschii	20	54	-	4	-	19

Alewives · *Alosa pseudoharengus*

As with many of the anadromous species, the diet of the alewife is much better understood in the freshwater environment than the marine. The alewife feeds visually, actively selecting larger sizes, and passively by filter feeding (Stone and Jessop, 1994). The fish enter fresh water in May to spawn and are harvested in large numbers as they travel upstream. The alewife is a major component of the gaspereau fishery in St.

Georges Bay (Kenchington, 1980). Adults may remain in fresh water for a period and some populations exist in land-locked conditions (Scott and Scott, 1988).

They are known to be abundant in areas of strong tidal mixing and upwelling. Diet studies for the Bay of Fundy, Scotian Shelf and Georges Bank (Stone and Jessop, 1994) have found the vast majority of prey to be crustaceans. Krill of chiefly two genera, *Meganyctiphanes norvegica*, and *Thysanoessa* spp., as well as amphipods are significant in the diet. Table 12 presents data from Stone and Jessop (1994) and from Georges Bank and New England by Bowman et al. (1976). Comparison of this data reveals different trends in feeding between sites. Krill was not the dominant food for Georges Bank and New England alewives, but instead arrow worms and mysids were a large part of the alewife diet, however, Gulf of Maine and western Nova Scotian alewife diets reflected Stone and Jessop's findings.

Table 12: Stomach contents of alewives collected from the Northwest Atlantic, percent volume,1990-1991 (Stone and Jessop, 1994) and percent weight, 1969-1972 (Bowman et al., 1976).

	Scotian Shelf, Georges Bank, Fundy Stone and Jessop, (1994)	S. New England Bowman et al. (1976)	Georges Bank Bowman et al. (1976)	Gulf of Maine Bowman et al. (1976)	Western. Nova Scotia Bowman et al. (1976)
Algae	**0.2**	.	.	.	.
Polychaetes	**0.5**	.	.	.	.
Molluscs	**0.3**	**56**	-	-	-
Pteropods	0.3	56	-	-	-
Crustaceans	**97.3**	**11.5**	**94**	**100**	**83**
Krill	91	-	13	100	79.7
Copepods	1.2	2.7	0.1	-	-
Amphipods	4.8	0.5	2	-	-
Mysids	0.2	0.3	75.6	-	-
Unidentified	.	8	2.4	-	3.3
Arrow worms	**< 0.5**	**31.2**	-	-	-
Tunicates	-	-	**3.7**	-	-
Fish	-	-	-	-	**15.4**
Fish larvae	**1.4**	.	.	.	.
Unidentified	0.8	1.3	2.3	-	1.6
No. stomachs	68	40	52	22	22
% empty	.	5	9.6	4.5	22.7

Significant variation in diet throughout size classes was not found. Feeding activity was observed in the Bay of Fundy to be greatest in the summer and lowest in the winter, but on the Scotian Shelf feeding intensity was highest in the winter. Seasonal variation in prey type was not clearly demonstrated (Stone and Jessop, 1994).

Stone and Daborn (1987) found alewife diet in Bay of Fundy estuaries to demonstrate selection of large benthic prey. Krill, calanoid copepods, amphipods, arrow worms, mysids, pteropods, decapod larvae and salps were fed upon. These authors believed that the selection of large prey was a reflection of availability, not prey preference.

Blueback herring · *Alosa aestivalis*

Blueback herring are not easily distinguished from alewife, thus their habits have not been well documented. They complete the same life cycle as the alewife, but return immediately to the sea after spawning. A small portion of the gaspereau harvest is contributed by this species (Chaput, 1993). Blueback herring are known in the marine environment to make upward migration at night and downward in day, reflecting the daily movements of the plankton. Copepods, amphipods, and mysids, are known to be consumed by the blueback herring, but Scott and Scott (1988) describe some disagreement as to the similarity of the diets of the blueback herring and alewives. Studies have illustrated identical diets, but others report heavier reliance on microzooplankton by herring, as opposed to alewives, which consume larger benthic plankton.

American Shad · *Alosa sapidissima*

The American shad travels to fresh water only to spawn, and is believed to return to sea immediately, thus spending most of its life in the marine environment. This fish overwinters from Florida to the Gulf of Maine and travels northward for the summer (Dadswell, 1986). They are present in the bay in mid-May and are found among the gaspereau run in June in the St. Georges Bay. Biomass in the bay was estimated to be 'a few hundred tons' in 1980 (Kenchington, 1980).

Marine feeding is not well documented. American shad are known to feed opportunistically on whatever is available in abundance. Copepods and mysids constitute a large proportion of the shad diet, particularly mysids among adults. In the Bay of Fundy, ostracods, isopods, insects, small smelt and sand lance were also reported as diet items (Scott and Scott, 1988).

SCOMBRIDAE

Atlantic mackerel · *Scomber scombrus*

Atlantic mackerel are an active pelagic schooling fish which overwinter in deep waters along New England to the Sable Bank, and in the spring move inshore either to the New England coast or within the Gulf of St. Lawrence. In the Gulf, spawning occurs from mid-June to mid-July, predominantly around the Magdalen Islands and the southern Gulf. The degree of their abundance is not known in St. Georges Bay, but they are suspected to be a significant component of the pelagic system (Kenchington, 1980). Mackerel are filter feeders, which also actively select prey. They feed heavily in the spring on plankton, amphipods, krill, crab larvae, small squid, and small fish, including mackerel (Scott and Scott, 1988).

Gregoire and Castonguay (1989) examined mackerel diet throughout the Maritimes. Southern Gulf sites within this study were located on Prince Edward Island and Baie des Chaleurs. Diet data from these sites are presented in Table 13. Calanoid copepods were present in over half of the stomachs and *Temoridae* were present in greater than 70% of stomachs at both sites. Amphipod and krill consumption was observed to be greater in the Baie des Chaleurs, replaced by nematode consumption in P. E. I., but generally the data from specific sites was not found to vary considerably from the regional diet pattern.

In Newfoundland, Moores et al. (1975) found mackerel to have a less diverse diet, which differed considerably in the occurrence of capelin in 66% of the stomachs and krill in 12% of mackerel stomachs.

Table 14 presents prey items of Atlantic mackerel collected from New England waters by Bowman et al (1976), who reported significant variation among sites. Although up to 25 % of the stomach contents were unidentified, clearly southern New England mackerel relied heavily on pteropods (57.8 % by weight) while Georges Bank and Gulf of Maine mackerel consumed 67.8 % and 76.4 % crustaceans by weight, respectively. Georges Bank diet was composed of 51.8 % krill, and Maine diet was composed of 76.4 % copepods.

Investigations by Kulka and Stobo (1981) of Scotian Shelf and Georges Bank mackerel diet found amphipods to comprise a large proportion of the diet, representing 62 % weight (fish larvae was second in weight at 17 %; additional food was krill, copepods and *Limacina* sp).

Kulka and Stobo (1981) found that the smallest mackerel, age-group 0, consumed 47 % by weight of krill, *M. norvegica* chiefly, and also *T. inermis*. The amphipod, *Parathemisto* contributed 22 % of the diet. At age group 1 and 2, amphipods contributed most to the mackerel diet (69% and 62% respectively).

Table 13: Percent occurrence of prey items of Atlantic mackerel from the Gulf of St. Lawrence (Gregoire et Castonguay, 1989) and Newfoundland (Moores et al., 1975).

	Prince Edward Island Gregoire et Castonguay, (1989)	Baie des Chaleurs Gregoire et Castonguay, (1989)	Average of all sites Gregoire et Castonguay, (1989)	Newfound-land Moores et al., (1975)
Kinorhyncha	-	-	**0.73**	·
Nematodes	**45.59**	**26.67**	**38.90**	·
Molluscs	**2.94**	**6.67**	**6.70**	**1**
Copepods	·	·	·	**1**
Calanidae	50.00	23.33	34.02	·
Other calanoida	67.74	76.67	57.83	·
Centropagidae	10.29	13.33	18.80	·
Pseudocalanidae	19.2	33.33	30.30	·
Temoridae	70.59	86.67	69.13	·
Other copepods	10.29	6.67	9.03	·
Amphipods	-	**13.33**	**11.94**	·
Mysids	-	-	**0.61**	·
Krill	**2.94**	**26.67**	**10.64**	**12**
Decapods	**26.47**	**40.00**	**33.88**	**2**
Branchiopods	**20.59**	**20.00**	**26.12**	·
Cirripedia	**14.71**	**3.33**	**4.15**	·
Other invertebrates	-	**3.33**	**1.78**	·
Fish, capelin	·	·	·	**66**
Fish eggs	**45.59**	**43.33**	**26.63**	·
Unidentified larva	66.18	46.67	61.14	·
Scales	13.24	3.33	39.25	·
Other	1.47	-	4.96	15

As with herring, there is a strong pattern of seasonal variation in feeding activity in mackerel. In Newfoundland, feeding was most intense in July, the proportion of empty stomachs being lowest, at 36%. In June and August feeding was moderate and in October, mackerel stomachs were found to be 95 % empty. From June to August, capelin, which are plentiful at the time are heavily fed upon. During September and October planktonic organisms, primarily krill, which are then plentiful, are consumed in greater quantity (Moores et al., 1975).

Table 14: Stomach contents of Atlantic mackerel (percent weight) collected in the Northwest Atlantic from 1969 to 1973 (Bowman et al., 1976).

	S. New England	Georges Bank	Gulf of Maine
Crustaceans	**5.8**	**67.8**	**76.4**
Gammarid amphipods	-	0.1	-
Hyperiid amphipods	0.4	-	-
Caridean shrimp	0.1	11.5	-
Penaeid shrimp	0.1	-	-
Anomuran crab	-	0.1	-
Krill	3.6	51.8	-
Mysids	-	2.2	-
Copepods	1.2	1.9	76.4
Unidentified	0.4	0.2	-
Molluscs	**57.8**	**1.0**	-
Pteropods	**57.8**	**0.4**	-
Cephalopods	-	**0.6**	-
Echinoderms	**0.8**	-	-
Brittle stars	0.3	-	-
Unidentified	0.5	-	-
Arrow worms	**0.8**	**2.3**	-
Tunicates	**6.2**	**7.9**	-
Fish	**3.6**	**0.8**	-
Sand lance	2.2	-	-
Gadids	-	-	-
Fish eggs	0.7	-	-
Unidentified	0.7	0.8	-
Animal remains	25	20.2	23.6
Stomachs	193	56	1
Percent empty	30.6	37.5	0

Bluefin tuna · *Thunnus thynnus*

The bluefin tuna enters Canadian waters during the summer and is found in the St. Georges Bay in September. The Gulf is the northern extent of its distribution, and although it is present for just a short period, it is a voracious and active carnivore.

Because it maintains its muscle tissue temperature at 10 to 15°C above water temperature, the bluefin tuna eats frequently. Tuna feed on schools of herring, capelin, mackerel, squid, saury, lanternfish and barracudinas (Scott and Scott, 1988). There were no reports found for the study area of tuna diet.

Atlantic Bonito · *Sarda sarda*

This species is thought to be uncommon in St. Georges Bay (Kenchington, 1980). Diet information was not found, although members of the Scombrid family are characterized as predatory fish that feed in schools on small fish and squid, or plankton in the case of smaller members (Scott and Scott, 1988).

OSMERIDAE

Capelin · *Mallotus villosus*

Capelin is typically abundant north of the Laurentian channel (Dunbar et al., 1980), and is a very important feature within an ecosystem as a link between the invertebrate base of the food web and fish, bird and marine mammal predators (Scott and Scott, 1988). Capelin has a limited presence in St. Georges Bay, occasionally in great abundance. In 1975, the first reported capelin spawning occurred in the bay; similar erratic spawnings have occurred elsewhere in Nova Scotia (Lambert et al., 1982b).

Capelin in the estuary/Gulf of St. Lawrence have been found to feed almost exclusively on zooplankton (Table 16), of this group, krill, chiefly *T. raschii* is the dominant biomass. Copepods, *C. Finmarchicus, T. longicornis*, and *P. minutus* are also significant in numerical terms, as well as appendicularians (Vesin et al., 1981). Chan and Carscadden (1976), report on capelin feeding in Labrador in 1973. Here, copepods and amphipods were the groups most heavily preyed upon, but fish larvae, thecosomes, ostracods, and arrow worms were also consumed. Kovalyov and Kudrin (1973) report capelin diet in the Grand Banks to generally reflect the findings of Vesin et al. (1981), with the exception of a greater reliance on amphipods as prey (Table 15).

Estuary and Gulf of St. Lawrence juveniles feed on small copepods (*T. longicornis, P. Minutus* and *Oithona* sp.), and krill and appendicularians to a lesser degree. At 140 mm in length, capelin shift from these small prey to larger items, particularly adult krill (Vesin et al., 1981). On the Grand Banks, copepods, chiefly *C. finmarchicus* are consumed by all age classes, however, the krill species *T. raschii* is consumed more by mature capelin. When krill are not abundant, juvenile sand lance and capelin are consumed (Gerisimova, 1994).

Vesin et al. (1981) found seasonal variation in feeding intensity in the Gulf region, observed as a relatively small number of empty stomachs (36 %) in May, and 83 % occurrence of empty stomachs when spawning. Few adult post-spawning capelin were sampled, this was attributed to heavy mortality of adults after spawning in spring. Their consumption is rapidly replaced by juveniles, which feed actively through spring and summer. A seasonal shift in type of prey consumed was also reported by Vesin et al. (1981) as a reduction in krill consumption and increase in copepods through summer.

Capelin in Atlantic sites are found to rely more upon amphipods and fish larvae as prey than in the Gulf, although these prey are also abundant in the estuary and Gulf of St. Lawrence (Gerisomova, 1994).

The population of planktivores with a short life cycle can fluctuate significantly. Although capelin are not generally abundant in St. Georges Bay, implications of capelin population fluctuations discussed by Gerasimova (1994) are relevant particularly to the more abundant mackerel and herring populations of the bay.

Table 15: Percent occurrence of prey groups of capelin in the estuary and Gulf of St. Lawrence (Vesin et al., 1981) and the Grand Banks (Kovalyov and Kudrin, 1973).

	Estuary and Western Gulf of St. Lawrence	Grand Banks March to June 1972
Krill	**33.4**	**44.1**
Thysanoessa raschii	17.0	·
Thysanoessa inermis	6.0	·
Thysanoessa sp.	5.3	·
M. norvegica	0.9	·
Unidentified	5.0	·
Krill juvenile	6.9	·
Copepods	**53.2**	**55.4**
Calanus finmarchicus	40.3	55.4
Calanus hyperboreus	13.6	·
Euchaeta norvegica	23.1	·
Metridia longa	22.1	·
Other large calanoids	5.9	·
Temora longicornis	22.3	·
Pseudocalanus minutus	16.4	·
Other small calanoids	13.9	·
Oithona sp.	10.0	·
Other crustaceans	**17.7**	**31.5**
Ostracods	3.4	·
Harpacticoid copepods	2.2	·
Hyperiid amphipods	5.1	31.5
Nauplii	7.2	·
Krill Larvae	1.5	·
Krill eggs	3.2	·
Other food types	**19.0**	**19.3**
Invertebrate eggs	7.2	·
Mollusc Larvae	6.4	·
Arrow worms	4.0	12.3
Larvacea	25	·
Ctenophores	·	0.8
Fish eggs	29	2.4
Fish Larvae	1.8	3.8

Gerasimova (1994) estimated the amount of zooplankton that became available to the Grand Banks ecosystem as a result of capelin year-class failure to be 294,000 tonnes/day during the period of 1972 to 1979. He states that there are implications of increased food availability in terms of populations of other planktivores, as populations at higher and lower trophic levels will experience reduced numbers of prey or predators, respectively. Vesin et al. (1981) estimates this value to be 150,000 tonnes/day for his study area, and suggests that the increase in short-finned squid population in Newfoundland was a response to the depressed capelin population.

Gerisimova (1994) suggests that the success of spring feeding in the Grand Banks is associated with the abundance of *C. finmarchicus*, which is generally a stable population. The abundance of krill species in capelin diet fluctuates considerably between years, but capelin were found to feed almost exclusively on *T. raschii.* This feeding preference was also observed in the St. Lawrence. The preference for *T. raschii* was thought to be a function of prey distribution. *T. raschii* is a herbivore, found in dense concentrations, other krill species which are predacious usually have a dispersed distribution (Gerisimova, 1994).

Because of the yearly variation in prey populations, trophic links are believed to be labile in spring, but feeding intensity is more stable. Ponomareva (1990), cited in Gerisimova (1994), has found that krill constitute a large proportion of the diet of the prespawning population. This was also in documented in the Gulf of St. Lawrence by Vesin et al. (1981).

Feeding was observed to have a daily cycle, peaking in morning and evening, except in the winter when just one daily peak was observed. For most of the year, capelin remain in schools at sea-bottom during the day. Feeding occurs during the vertical migration, which corresponds to the vertical migration of many planktonic crustaceans (Gerisimova, 1994). Another variable in feeding patterns observed in the Georges Bank was spatial division in the water column and over area between adult and juvenile capelin.

American smelt · *Osmerus mordax*

This anadromous fish carries out its spawning run in May, and is believed to return to sea shortly after, followed by its young. The American smelt population remain in the estuaries of St. Georges Bay over winter (Kenchington, 1980). It is an important source of food for marine fish such as cod and salmon as well as seals and aquatic birds (Scott and Scott, 1988).

American smelt feed upon any available food; amphipods, krill, mysids, shrimp, marine worms and other small fish such as mummichogs, silversides, and herring. The young feed more selectively, eating smaller items, and feed more on fish as they grow (Scott and Scott, 1988).

Atlantic Salmon · *Salmo Salar*

Atlantic salmon hatch in spring in freshwater streams surrounding the Gulf of St. Lawrence and after 2 or 3 years begin to migrate annually to the Atlantic Ocean to overwinter, returning to streams in the spring to spawn. Marine diet includes chiefly krill, but also amphipods and decapods (Scott and Scott, 1988). They have been thought to have little impact on the marine ecosystem of the Gulf of St. Lawrence as it was believed that they move immediately to the ocean once leaving the rivers (Dutil and Coutu, 1988).

There have been several accounts of young Atlantic salmon being recovered in herring gill nets in late summer and autumn within the Gulf (Dutil and Coutu, 1988). Postsmolts, or young salmon, leaving the river for their first ocean migration enter the Gulf in early summer and thus a certain number are known to feed within the Gulf ecosystem for the summer season. During this period they average 1.65 mm/day increase in mean length (Dutil and Coutu, 1988). Because the salmon in Fundy, Gulf of Maine and on France's coast are known to linger along the coast before migrating offshore, Dutil and Coutu (1988) state that 'the presence of postsmolts near shore in autumn ... is a characteristic of the marine life of the Atlantic salmon in North America". No reports were found of this behavior occurring within St. Georges Bay.

Over the period of 1982 to 1985, the stomach contents of bycatch and experimental catches of postsmolt Atlantic salmon from the northern Gulf of St. Lawrence were analyzed by Dutil and Coutu (1988). The postsmolts and 1 and 2-year salmon appeared to feed more actively at dawn and dusk and travel near the surface while remaining in the coastal area. Occurrence of prey in salmon stomachs from this study are presented in Table 16.

Table16: Percent occurrence of prey groups in stomachs of marine postsmolt Atlantic salmon in northern Gulf of St. Lawrence in 1982 (Dutil and Coutu, 1988).

	Percent Occurrence
Fish	90
Fish - sole contents	84
Capelin	10
sand lance	92
Invertebrates- sole contents	26
Insects	3
Crustaceans	23
No. stomachs	373
% empty	29.2

Small fish, predominantly sand lance, 70 – 80 mm in length, are the most numerous contributors to the marine salmon diet in the northern Gulf. Of the crustaceans consumed, krill was found to represent 68 % of their numbers, while decapods and amphipods contributed 24 % and 8 % respectively. Variation over the summer in diet was observed as an increased reliance on small sand lance and krill (*M. norvegica)*. Low diversity of prey selection was observed in this study as opposed to a diverse diet in the North Atlantic salmon population. Dutil and Coutu (1988) cite Lear (1972) and Reddin (1985), showing great variation in Atlantic salmon diets between the coast of Newfoundland and the Grand Banks, suggesting that salmon are not selective predators.

The marine diet regime described by Dutil and Coutu (1988) diverged significantly from that of salmon taken from an estuary in the same study. Small fish were only present in 5 of the 39 estuarine salmon stomachs containing food, and insects and crustaceans were present in 87 % and 92 % of the stomachs, respectively.

Brook trout · *Salvelinus fontinalis*

Brook trout are an anadromous species that feed heavily while remaining inshore in their marine phase. In the marine environment they are carnivorous, and feed on silversides, mummichogs, rainbow smelt, small eels, sea raven, rock gunnel, and invertebrates such as amphipods and sandworms (Scott and Scott, 1988).

ANGUILLIDAE

American eel · *Anguilla rostrata*

The American eel is a diadromous species that spends its juvenile years in fresh water or estuaries, and travels to the ocean to breed. The eel moves seasonally upstream and downstream, taking advantage of the warmer water of the estuary in the winter. Some reside in the estuary throughout the year, and some travel to marine waters for the summer (Cameron et al., 2000).

Although the American eel supports a substantial fishery in estuaries of St. Georges Bay, there is very little known about its marine existence. No studies were found for marine diet, but they are known to consume plankton as marine larvae (Eales, 1968), and are carnivorous bottom feeders, eating plankton, crustaceans, blue crab, polychaete worms, and soft-shelled clams in estuaries (Scott and Scott, 1988).

SCOMBERESOCIDAE

Atlantic saury · *Scomberesox saurus*

The Atlantic saury is found in open warm surface waters; it is a schooling fish which undertakes diurnal vertical migrations. It feeds on zooplankton, the composition of which depends on the size of predator, the prey available and the season. Copepods, krill, and amphipods, as well as fish eggs and larvae make up the saury diet. Feeding intensity increases in the summer and decreases in autumn. This fish is an important diet component for large predators, such as cod, pollock, tuna, dolphins, and porpoises (Scott and Scott, 1988).

XIPHIDAE

Swordfish · *Xiphias gladius*

The swordfish is an aggressive, opportunistic feeder, foraging from various trophic levels (Stillwell and Kohler, 1985). It is known to rest on bottom during day, although sometimes it is found basking at the water surface, perhaps for warmth. Diurnal migrations coincide with migration of mesopelagic species. In Canadian waters, prey includes mackerel, barracudinas, silver hake, redfish, herring, lanternfish and squid (Scott and Scott, 1988). Squid has been thought to be a relatively unimportant prey group, but evidence to the contrary is presented by Stillwell and Kohler (1985) in Table 17. Swordfish are thought to be uncommon in St. Georges Bay (Kenchington, 1980).

The sword is used in feeding; fish that would be too large to ingest whole are found in pieces in swordfish stomachs, also, ingested fish show signs of blows and slashing. This adaptation drastically reduces the restriction of prey size on prey selection. Stillwell and Kohler (1985) estimated the food volume ingested daily was 1 % of the swordfish's body weight, which is equivalent to 199 kg per year. These authors also noted that it shares the same trophic levels as blue shark, demonstrated by similarities in prey.

Data presented in Table 17 is collected from along the Atlantic coast from southern New England to the Grand Banks. Stomach contents represent a diverse diet, with a selection of prey from throughout the water column. The silver hake, a benthic fish, which comprises the largest proportion of the swordfish diet, is believed to be consumed when it leaves the bottom at night. Cod and haddock are also consumed. The quantity of squid consumed was equivalent in volume to fish. The prevalence of consumed squid found, relative to earlier studies, is thought to be a result of greater abundance of squid at the time of the study (Stillwell and Kohler, 1985). No differences in diet by size or sex were observed.

Table 17: Prey of the swordfish, Northwest Atlantic waters, Stillwell and Kohler (1985).

	Percent Volume
Cephalopods	
Ommastrephidae	20.70
Short-finned squid	25.46
Octopoteuthidae	0.26
Onychoteuthidea	0.14
Unidentified	20.70
Fish	
Silver hake	9.43
Atlantic mackerel	5.41
Cod fishes	2.62
Blue fish	4.01
Sand lance	0.16
Butter fish	1.53
Bigeye cigarfish	0.64
Snake mackerel	0.2
Lancet fish	0.52
Atlantic menhaden	0.49
Duckbill barracudina	0.26
Red fish	2.35
Scorpion fish	0.34
Atlantic herring	0.17
Unidentified	4.16
Miscellaneous	**0.16**

CHARCHARIIDAE

Blue shark · *Prionace glauca*

Blue sharks are rarely seen and possibly uncommon in St. Georges Bay waters. Pelagic fish and squid are consumed in greatest proportions by blue sharks, although some benthic fish are consumed. Herring, silver hake, white and red hake, cod, haddock, pollock, mackerel, butterfish, sea raven and flounders are prey of the blue shark (Scott and Scott, 1988).

LAMNIDAE

Porbeagle · *Lamna nasus*

The porbeagle shark feeds on pelagic schooling fish such as herring, gaspereau (alewife and blueback herring) and mackerel in greatest quantity, but gadids, haddock, cusk and squid are also prey items (Scott and Scott, 1988).

SQUALIDAE

Spiny dogfish · *Squalus acanthias*

The Spiny dogfish is very common to the southern Gulf of St. Lawrence, but no evidence of its occurrence in St. Georges Bay was found during extensive sampling by Kenchington (1980). Scott and Scott (1988) describe spiny dogfish as opportunistic feeders, preying mostly upon small fish, including any fish smaller than themselves.

STROMATEIDAE

Butterfish · *Peprilus triacanthus*

The butterfish, a warm-water schooling fish, has a varied diet including small fish, squid, amphipods, shrimp and marine worms (Scott and Scott, 1988). New England and Georges Bank butterfish have been examined by Bowman et al. (1976), who reported the importance of sea squirts (tunicates) as a prey group (Table 18). The New England population consumed a diet comprised of 76.4 % by weight of sea squirts, amended with small amounts of crustaceans, annelids, and arrow worms. Crustaceans contributed a much larger proportion of the diet of butterfish on the Georges Bank (37.8 %; 7 % being krill, although much of the crustacean component was unidentified). Sea squirts contributed just 21.4 % to the Georges Bank diet, but the substantial amount of unidentified remains results in some uncertainty in comparison of the two sites.

Table 18: Stomach contents of butterfish, collected from southern New England and Georges Bank, percent weight.

	S. New England Bowman and Michaels (1984)	S. New England Bowman et al. (1976)	Georges Bank Bowman et al. (1976)
Annelids	**20.3**	**2.9**	-
Crustaceans	**12.0**	**2.4**	**37.8**
Amphipods	0.9	-	0.9
Decapods	3.4	0.4	0.1
Isopods	.	0.1	-
Krill	.	0.1	7.5
Copepods	6.9	0.1	0.1
Unidentified	0.8	1.7	29.2
Thaliacea	**8.5**	.	.
Arrow worms	.	**5.1**	**7.5**
Sea squirts	.	**76.4**	**21.4**
Animal remains	58.6	13.2	33.3
No. stomachs	394	359	67
% empty	27.4	46.5	40.3

PETROMYZONTIDAE

Sea lamprey · *Petromyzon marinus*

In the marine environment, sea lamprey prey upon cod, haddock, hake, American shad, salmon, sturgeon and swordfish by attaching to their bodies and ingesting blood and flesh (Scott and Scott, 1988). They are suspected to occur regularly in St. Georges Bay, but were not found in extensive sampling of the bay (Kenchington, 1980).

MOLIDAE

Ocean sunfish · *Mola mola*

The ocean sunfish is typically a southern species which enters the Gulf of St. Lawrence as the northern limit of its distribution during the summer. It feeds on jellyfish, comb jellies, crustaceans, molluscs, brittlestars, and other various items. (Scott and Scott, 1988).

1.c Coastal / Estuarine Pelagic Fish

CYPRINODONTIDAE

Mummichog · *Fundulus heteroclitus*

Mummichogs are abundant in brackish areas of the St. Georges Bay (Kenchington, 1980). They are an estuarine omnivore that forages among vegetation, consuming small crustaceans, polychaetes, insect larvae, small fish, vegetation and eggs of other fish and its own (Scott and Scott, 1988).

Banded killifish · *Fundulus diaphanus*

The banded killifish is a resident of St. Georges Bay (T. Lambert, pers. comm.) and is chiefly a freshwater species, but is known to be salinity tolerant and occasionally occurs as a sympatric population with the mummichog. Specific diet information was not found, however, members of Cyprinodontidae are known to feed on small crustaceans, chironomid larvae, fish eggs and larvae, vegetation, flatworms and insects (Scott and Scott, 1988).

ANTHERINIDAE

Atlantic silversides · *Menidia menidia*

Atlantic silversides are a common coastal resident, also inhabiting estuaries and bays of eastern Canada. They tend to associate with sandy or gravelly shores during summer, and move offshore for the winter. Those in St. Georges Bay remain in the bay for the winter (Kenchington, 1980). Scott and Scott (1988) describe silversides as an omnivore, feeding on copepods, mysids, shrimp, small squid, marine worms, eggs of their own species, and insects when other food is less abundant.

Regional studies of silverside diet were identified for summer and fall inshore coastal feeding in 1979 in the Minas Bay, Bay of Fundy, and inshore and offshore populations in winter off the New Jersey Coast in 1989.

Gilmurray and Daborn (1981) present data graphically over several sampling times, thus their findings will be discussed in general terms. Copepods, particularly, *Eurytemora herdmani* were preyed upon more heavily in the spring and fall. During the summer, amphipods (*Corophium* sp.) and cumaceans contributed larger proportions of the diet, although in varying proportions. The seasonal variation in diet was thought to reflect abundance of prey, as copepods were less available during the summer.

The percent of biomass of various prey groups varied with size group of the predator. Cumaceans were the exclusive prey for silversides from 21 – 40 mm, and thereafter, larger fish constituted about half of the prey. Diet included copepods, and isopods. Silversides larger than 100 mm mainly fed on amphipods, but also consumed a significant amount of insects along with small amounts of cumaceans and copepods (Gilmurray and Daborn, 1981).

Winter represents the period during which feeding by Atlantic silversides is at a minimum. Winter diet, presented in Table 19 (Anonymous, 1989) illustrates the importance of copepods at both inshore and offshore sites. A comparison of diets of these sites reveals that although the prey is the same, there is a drastic shift in proportion of prey types ingested between the two ecosystems. Mysids constitute 70.31 % volume of offshore diet, as opposed to 17.83 % inshore, whereas copepods contribute 24.79 % to offshore diets and 82.17 % to inshore diets. This variation was explained as being a result of differences in feeding depths. Inshore feeding occurs higher in the water column, while offshore feeding is at greater depths, thus the prevalence of epibenthic mysids. There is also a greater diversity in offshore diet (Anonymous, 1989).

Table 19: Winter diet of Atlantic silversides collected from New York State in 1986, Anonymous (1989), percent volume.

	Offshore New York Bight	Inshore salt marsh Long Island Sound
Mysids	**70.31**	**17.83**
Mysidopsis bigelowi	69.64	0.03
Neomysis americana	0.67	17.65
Hetero formosa	-	0.15
Copepods	**24.79**	**82.17**
Temora sp.	20.57	77.27
Acartia sp.	4.22	4.9
Cumaceans	**2.02**	-
Oxyurostylis smithi	2.02	-
Amphipods	**0.67**	-
Nauplii barnacle larvae	**2.19**	-
Number of stomachs	68	114

GASTEROSTEIDAE · STICKLEBACKS

Four species of sticklebacks are reported in St. Georges Bay (Kenchington, 1980); the threespine stickleback (*Gasterosteus aculeatus),* blackspotted stickleback, (*Gasterosteus wheatlandi),* fourspine stickleback (*Apeltes quadracus*), and the ninespine stickleback (*Pungitius pungitius).* The former two species combined, are believed to be among the most abundant brackish and inshore fish in St. Georges Bay, while the abundance of the ninespine is unknown (Kenchington, 1980).

The Gasterosteidae family is anadromous, but includes some members that live almost completely in marine conditions as well as those that are freshwater dwellers. The family is predacious, and feed largely on small invertebrates, fish and fish eggs (Scott and Scott, 1980).

Marine pelagic diet has been reported by Williams and Delbeek (1989) for the threespine and blackspotted stickleback in the Bay of Fundy. The threespine stickleback is chiefly anadromous, while the blackspotted stickleback is marine, breeding in brackish waters. Generally sticklebacks overwinter in deep water; the degree to which they utilize the warm, prey-rich inshore waters for foraging varies. Large fish predators are less prevalent here, while shorebird predation would be expected to be heavier (Williams and Delbeek, 1989).

The two species' diets were qualitatively similar as reported in Table 20. Of interest is that the significant prey of these sticklebacks in the Bay of Fundy, *Centropages typicus* and *Eurytemora* cf *americana* were not the most abundant prey available. *Calanus finmarchicus* and *Anomaloceraa opalus* are the most prevalent copepods, but are both larger than 2.3 mm, while the mean gape of the sticklebacks collected were 1.9 mm. The dominant prey ranged in size from 0.6 – 1.8 mm. Thus prey selection appears to limited by gape size.

Table 20: Diet composition of stickleback species in the Bay of Fundy
Williams and Delbeek (1989), percent volume*

	Threespine	Blackspotted
Calanoida	75.3	80.4
Nauplii	1	0
Cladocera	3.1	11
Planktonic eggs	2.7	0.8

*Data presented here has been averaged from data for three sites presented in study

Delbeek and Williams (1988) describe sticklebacks as opportunistic feeders, attributing changes in diet to changes in prey density, rather than preference. In their investigation of feeding selectivity of threespine, fourspine, ninespine and blackspotted stickleback species, they observed differential prey selection and morphological constraints (gape) which served to reduce competition among these species within the same ecosystem.

Fourspine sticklebacks are mainly marine species, and feed on planktonic gammarids, isopods, chironomids, and plants. The ninespine is also a marine-brackish water inhabitant and feeds on insects, small crustaceans, and eggs and larvae of their own species (Scott and Scott, 1988).

SYNGNATHIDAE

Northern pipefish · *Syngnathus fuscus*

The northern pipefish is a summer resident in shallow seagrass (*Zostera marina*) beds in coastal areas, arriving from deep water channels in early spring and returning in late fall (Ryer and Orth, 1987). Their impact on the St. Georges Bay food web is therefore confined to coastal communities. Feeding is carried out by actively approaching prey while engaging a sucking action.

Diet is reported from coastal areas south of Cape Cod. The northern pipefish diet is composed mainly of small crustaceans such as amphipods, isopods and copepods. Prey selection is believed to be influenced by gape size, as Ryer and Orth (1987) found that prey consumed were the smaller members within species available in the field from Chesapeake Bay. They are described by Nelson (1979) as having "extremely small mouths and are incapable of consuming large amphipods". Results from Ryer and Orth's study are presented in Table 21.

Table 21: Diet of northern pipefish in percent dry weight by month, Chesapeake Bay, 1979, from Ryer and Orth (1987).

	May	June	July	Aug.	Sept.	Oct.	Nov.
Calanoid copepods	0.03	5.11	87.33	58.34	9.02	1.68	31.03
Gammarus mucronatus	68.38	51.09	1.89	-	-	-	4.23
Erichsonells attenutat	-	1.96	0.54	23.34	49.72	61.76	-
Caprellid amphipods	21.16	14.57	-	1.17	1.10	0.42	51.64
Other gammarids	6.06	16.47	1.61	4.08	13.63	11.34	-
Other isopods	0.10	6.58	8.62	4.55	4.05	2.52	3.99
Mysid shrimp	-	0.27	-	1.28	-	-	0.47
Polychaetes	-	3.91	-	-	-	-	39.67
Other prey	4.2	-	-	7.24	22.47	22.27	-
No. Stomachs	18	23-	15	25	24	9	22

Amphipods were the dominant prey in May and June, while July and August consumption of copepods increased. Isopods were dominant in August and continued into the autumn, with other prey, to be a major prey a group. Percent dry weight was used for this study which would overestimate the importance of 'other prey' as many of them had calcified shells or tests.

Variation in diet by size was observed as a greater number of calanoid copepods being consumed by smaller fish than by large fish. There was a greater number of smaller fish at the early-season bloom of calanoids. Later in the season, smaller fish continued to select smaller prey.

Seasonal variation in diet observed in that study was attributed to changing prey abundance. There is evidence that decline in amphipod abundance in this ecosystem

coincides with peak predator abundance, suggesting that the amphipod population is greatly influenced by predation. Ryer and Orth (1987) found that the northern pipefish fed primarily on *Gammarus* and calanoid copepods when they were in great abundance, but then but fed extensively on *Erichsonella attenuata* only after the former populations were absent, indicating prey selectivity.

The pipefish offers a challenge in diet studies as the gastrointestinal tract is relatively undifferentiated. Ryer and Orth (1987) arbitrarily designated the first half of the tract as a collection area as the contents there were not extensively digested.

1.d Squid · *Illex Illecebrosus, Loligo pealei*

Squid are known to be occasionally present in the St. Georges Bay inshore in late summer and early autumn, and can be exceedingly abundant in some years (Kenchington, 1980). They do not, however, appear to be a prevalent item among the diet of fish studies within the southern gulf. Squid are important in Atlantic ecosystems as food prey for many larger fish, seals, and marine mammals. The degree of their impact on St. Georges Bay is unclear. It would be expected that opportunistic predators that have been demonstrated to eat squid in other regions would utilize the resource as it becomes available in the bay.

Considerable work has been done on two species of squid, the short-finned squid, *Illex illecebrosus* and long-finned squid, *Loligo pealei.* Vinogradov (1984), showed that fish and squid were major diet components of both squid species. Froerman (1983) had found that short-finned squid fed most on krill; and fish and squid were consumed in smaller quantities.

2. Feeding of Mesopelagic Fish

The Gadidae family is noted as existing within a range that encompasses both pelagic and benthic zones and is classified in various sources as pelagic, mesopelagic, or benthic. Local conditions probably contribute to variation within species, and particular species have tendencies towards different zones.

2.a GADIDAE

Atlantic cod · *Gadus morhua*

The Atlantic cod is the key fish predator in the southern Gulf of St. Lawrence (Majowski and Waiwood, 1980). Cod feed visually (Methven, 1999) on nektonic, epibenthic and shallow infaunal prey (Lilly, 1987). They are associated with cool temperate to subarctic waters on the continental shelf and inshore. Scott and Scott (1988) describe cod as voracious benthic feeders, which consume a diverse diet, fish being a large diet component with the type varying by locality.

In St. Georges Bay, cod are among the most abundant fish by biomass and are found in deeper waters, mainly below 30 m. Cod enter the bay and spawn during May; eggs hatch and develop into larvae and juveniles. Their population peaks in midsummer, while the population of juveniles peaks in August. Some, or all, Atlantic cod leave the bay in winter (Kenchington, 1980). The adult population migrates first to deeper water in the autumn, followed by the juveniles (Clay, 1991).

A series of diet studies have been carried out in the southern Gulf of St. Lawrence, predominantly in the western portion, but no sampling data has been found within St. Georges Bay. Waiwood (1981) reports on historical data of stomach content by percent volume for over 20,000 cod stomachs taken from 1959 to 1973 and 1979 to 1980, distributed across the southern Gulf of St. Lawrence. The data, presented in detail by predator size and year, is presented in Appendix 4. Sampling sites were not evenly distributed, thus the data is somewhat biased toward the southwestern portion of the Gulf.

This data suggests a concentration of prey, and of predation by cod in the southwestern Gulf, major species consumed being capelin, flatfish, herring, gadoids and mackerel. Invertebrates consumed were predominantly krill, amphipods, mysids, polychaetes, and the decapods *Crangon*, *Pandalidae*, *Pauridae*, *Hyas* and *Chionocetes*. Krill, polychaetes, bivalves, snails, brittlestars, and amphipods were found in large quantities in cod diet in the southeastern Gulf, as well as flatfish and herring in the late fall.

Waiwood (1981) suggests that the occurrence of predation of particular species could be interpreted as representative of prey distribution. Thus, the data presented provides a general assessment of prey distribution from 1959 to 1973 throughout the

southern Gulf. Despite the bias of sample sites to the western Gulf, there were clear differences in distribution of predation of various species. Capelin, mackerel and gadids were mostly restricted to the southwestern Gulf, but flatfish predation was more evenly distributed, and herring predation follows a pattern counterclockwise from the Laurentian Channel to the southern Gulf throughout the summer and autumn. Invertebrates were consumed throughout the southern Gulf, with a concentration in the west.

Much of the data pertaining to cod diet is presented by age group, in percent weight, and in earlier studies, in percentage occurrence. These factors hamper presentation of simple summary data, as well as the direct comparison of current to historical data. Table 22 presents diet information from the southwestern Gulf of St. Lawrence reported by Waiwood and Majowski (1984). Fish, particularly flatfish, crustaceans, chiefly decapods and krill, and also molluscs and annelids are all significant components of cod diet.

Table 22: Stomach contents of Atlantic cod from southwestern Gulf of St. Lawrence, adjusted to exclude unidentified categories, May to November 1980 (Waiwood and Majowski, 1984).

Age group	3.4	5	6	7	8	9-10	11+
Size (cm)	33.9-43.7	43.8-45.1	45.2-53.4	53.5-61.4	61.5-69.9	70.0-80.8	>80.8
Molluscs	**5.0**	**12.9**	**15.8**	**13.1**	**7.1**	**4.3**	**3.2**
Annelids	**9.2**	**6.8**	**5.3**	**3.0**	**3.4**	**1.8**	**2.1**
Crustaceans	**51.2**	**40.0**	**38.2**	**40.6**	**42.1**	**27.6**	**27.9**
Decapods	23.3	19.1	18.8	26.6	32.6	25.3	26.4
Pandalidae	1.9	2.0	0.9	1.4	0.8	0.1	1.1
Crangonidae	3.1	3.3	2.3	1.5	0.6	0.4	2.5
Majidae	6.7	5.6	8.5	16.9	29.0	24.0	21.5
Others	11.6	8.2	7.1	6.8	2.2	0.8	1.4
Krill	15.5	11.9	14.2	10.6	6.5	2.2	1.2
Mysids	5.0	2.9	1.3	0.8	1.5	-	0.1
Amphipods	7.5	6.1	3.9	2.6	1.4	0.1	0.2
Echinoderms	**2.0**	**3.3**	**5.0**	**5.0**	**3.8**	**2.2**	**2.3**
Fish	**15.9**	**21.2**	**19.2**	**23.1**	**33.8**	**58.8**	**60.9**
Flatfish	1.5	3.3	1.6	3.2	10.2	30.1	41.2
Gadids	-	0	-	0.3	1.3	11.0	12.1
Scombrids	-	0.4	0.4	1.5	3.1	6.8	6.9
Other	14.4	17.5	17.1	18.2	19.2	10.9	0.7
Commercial Species							
American plaice	1.5	3.3	1.6	2.7	10.2	19.5	27.1
Atlantic cod	-	-	-	0.3	1.3	6.6	7.1
Atlantic mackerel	-	0.4	0.4	1.5	3.1	6.8	6.9
Atlantic herring	-	-	-	0.9	1.6	4.4	-
Snow crab	1.0	1.5	4.5	12.2	22.3	18.2	14.7

Methven (1999) reviews diet studies of Atlantic cod and reports a general pattern reflected by the data presented in Table 22. Crustaceans and fish are always found to be the two most heavily consumed prey groups, with the former being fed upon more by smaller cod and the latter usually being consumed more by larger cod.

Kohler and Fitzgerald (1969) present data which illustrates similarities between Gulf of St. Lawrence (Magdalen Shallows), and Scotian Shelf cod diets. In both areas, there was a transition from consumption of mainly crustaceans by small cod to a fish diet with increased size. The different availabilities of prey between locations are reflected in a predominance of herring in Gulf diet, sand lance in Scotian Shelf diet (Kohler and Fitzgerald, 1969) and capelin in Newfoundland diet (Minet and Perodou, 1977). This flexibility in diet is common, as cod exhibits a preference for fish, particularly pelagic fish which are migratory and experience considerable variability in abundance between years (Methven, 1999).

Herring was found to be a significant contributor to the diet of cod in the 1950's and 1960's, (Kohler and Fitzgerald, 1969; Powles, 1958), however, Waiwood and Losier (1982) reported a reduction more recently in herring contribution to cod diet. They attributed earlier high consumption rates to an increase in herring availability due to increased vulnerability to predation because of disease. Their analysis revealed that the percentage of herring in cod diet was less than 1 % when the herring abundance was low, however, at peak population, herring never contributed more than 14% to cod diet. Thus it appears that cod will reach a saturation level for prey species, given increasing abundances.

Capelin consumption by cod has been investigated in several regions of the Northwest Atlantic. In the northern Gulf of St. Lawrence, Minet and Perodou (1977) reported capelin as contributing greater than 75% of the diet of smaller cod (26 to 55 cm), but in cod of lengths 76 to 115 cm, the percent weight of capelin was reduced to less than 25 %. Seasonal variation in diet was not observed to be substantial.

From 1977-78 area 4T (southern Gulf) diet data, Majowski and Waiwood (1980) calculated the maximal possible contribution of fish species to the cod diet as 14 % capelin, 2.8 % plaice, 0.2 % herring and 4.3 % for young cod.

Waiwood and Majowski (1984) found an increase in the consumption of fish, such as mackerel, cod, and flatfish with increase in predator size as well as increasing presence of larger crustaceans, such as *Crangonidae, Pandalidae*, and skates. Change in cod diet with size, was observed by Waiwood et al. (1980) as the prominence of pelagic prey such as krill, amphipods and capelin in small cod stomachs. Powles (1958) reports an increase in benthic prey with size, noting that they begin to actually 'root-up' bottom fauna at 31-50 cm in length.

Powles (1965) discusses the potential for competition in the Magdalen Shallows between cod and American plaice, both of which being abundant fish in St. Georges Bay Powles observed that more competition would occur among juveniles, as diet for both

species is less specialized at this stage. Because plaice diet becomes more specialized with age, feeding chiefly on echinoderms and molluscs, the unspecialized diet of cod reduces competition with plaice, and competition for prey is limited to larger crustaceans.

Diet of cod from May to November of 1980 in the southwestern Gulf was examined by Waiwood and Majowski (1984). Krill consumption was found to be highest in the spring, low in the summer and somewhat increased in the fall. In September and November, the contribution of fish is reduced while the proportion of snow crab and molluscs increased in cod diet. These authors suggest that significant changes in prey composition have corresponded to periods of optimum and sub-optimum feeding by cod, as the caloric content of prey species varies.

Silver hake · *Merluccius bilinearis*

Silver hake are an abundant benthic species in the Northwest Atlantic, feeding nocturnally, and preferring warmer water than other gadids (Scott and Scott, 1988). They are new-comers to St. Georges Bay, not commonly known to be in the Gulf of St. Lawrence before the 1950's (Kenchington, 1980). Studies reviewed suggest that they are opportunistic feeders which feed primarily on gadids, including young hake, and a variety of pelagic species and crustaceans, primarily krill. Because of their abundance and versatility in feeding, they are thought to have a considerable potential role in regulating the Northwest Atlantic ecosystem (Edwards and Bowman, 1979, cited in Waldron, 1987).

Diet has been examined on the Scotian Shelf and Georges Bank as well as Newfoundland, although information was not found for silver hake within the Gulf of St. Lawrence. All studies find crustaceans and fish to be major preys items. Selected studies are presented in Table 23.

Waldron (1987) found that although crustaceans are numerically significant on the Scotian Shelf (44 % frequency), fish contribute 48.5 % to the diet of silver hake by weight. Waldron reports that young silver hake represented 25.4 of these percentage points. High cannibalism rates are believed to reflect a pattern of silver hake eating whatever is abundant. He also noted that silver hake feed primarily on fish that are pre-recruit to the fishery. Vinogradov (1972) did not find such a high incidence of cannibalism, but acknowledged its prevalence among silver hake. His studies on the Scotian Bank and the Georges Bank reported anchovy, herring, argentines, mackerel and sand lance as most common prey.

Bowman and Michaels (1984) found fish consumption to range from 76.4 % to 78.4 % of diet weight, herring and mackerel constituting the largest proportions of the diet. Vinogradov (1972) found invertebrate prey to consist mainly of the krill species *M. norvegica* and *T. inermis*; but also included shrimp and squid; fish being consumed to a lesser degree than apparent in other studies.

Table 23: Stomach contents of silver hake stomachs (percent weight) reported from Scotian Shelf, Southern New England, Georges Bank, and Western Nova Scotia: (1) 1981-1986, Waldron (1987); (2) Bowman and Michaels (1984); (3) 1969-1972, Bowman et al. (1976).

	Scotian Shelf 1	S. New England 2	Georges Bank 2	S. New England 3	Georges Bank 3	Gulf of Maine 3	W. Nova Scotia 3
Annelids	**< 0.05**	**0.1**	**0.1**	**1.0**	-	-	-
Crustaceans	**20.3**	**7.3**	**16.4**	**36.7**	**20.5**	**21.3**	**33.8**
Amphipods	0.3	0.2	0.4	1.1	0.1	-	-
Krill	16.1	3.4	7.9	14.4	13.2	12.4	28.3
Mysids	.	0.7	1.2	0.7	-	0.2	0.1
Decapods	0.8	2.6	6.5	16.3	4.6	6.3	0.5
Cumaceans	.	0.1	< 0.1	0.1	-	-	-
Copepods	< 0.05	< 0.1	< 0.1	-	-	-	0.1
Unidentified	.	0.3	0.4	4.1	2.6	2.4	4.8
Molluscs (squid)	**23.5**	**13.0**	**6.7**	**0.8**	**0.6**	**1.3**	-
Echinoderms	**2.2**	.	.	.	.	.	.
Arrow worms	.	.	.	**0.1**	-	-	-
Fish	**48.5**	**78.4**	**76.4**	**58.8**	**78.2**	**76.2**	**65.0**
Gadids	27.0	.	.	11.7	-	1.4	51.1
Silver hake	25.4	7.9	0.4	.	.	.	.
Red hake	.	-	0.8	.	.	.	.
Mackerel	.	6	21.1	29.6	-	27.9	-
Herring	.	1.3	5	-	-	32.0	-
Amer. sand lance	**2.3**	0.4	4.8	.	.	.	.
Butterfish	.	2.2	8.9	.	.	.	.
Atlantic saury	.	-	6.1	.	.	.	.
Scup	.	4.1	-	.	.	.	.
Lanternfishes	2.5	.	.	.	.	.	.
Baracudina	1.1	.	.	.	.	.	.
Red fish	0.1	.	.	.	.	.	.
Flat fish	.	.	.	0.1	-	-	-
Other fish	0.9	56.5	29.3	.	.	.	.
Unidentified	14.7	.	.	17.3	78.2	14.9	13.9
No. stomachs	2855	918	915	707	236	409	284
% empty	23.9	38.9	29.3	33.7	26.3	34.7	33.5

Bowman and Michaels (1984) found crustaceans to contribute most to the silver hake diet. Among crustaceans, amphipods (*Ampeliscidae, Parathemisto)*, decapods (*Crangon septemspinosa* and *Dichelopandalus lepotcerus)* and krill (exclusively *M. norvegica*) constituted the greatest biomasses. The proportion of fish consumed reflected Langton and Bowman's findings, and squid also contributed a significant proportion of prey. Bowman et al. (1976) provide comparable data from the same sites sampled by Bowman and Michaels (1984).

Young silver hake feed heavily on crustaceans (Waldron, 1987; Vinogradov, 1983), although adult silver hake continue to prey upon this group. Molluscs (squid) are also eaten as a transition to larger prey, and fish contributes a greater proportion of diet with predator age. The size of prey also increases with hake size. Bowman et al. (1987) found that young silver hake fed on amphipods (*Caprillidae* and *Parathemisto),* decapods (*Crangonidae),* mysids (*Neomysis americana),* and krill (*M. norvegica)* as well as small fish including silver hake and sand lance.

Seasonal variation in silver hake diet is attributed to fluctuation in abundance rather than varying predator preference. Waldron (1987) observed a shift in diet from predominantly fish in the spring to a mixture of fish, crustaceans and molluscs during the summer and a return to fish predominantly in the fall. As silver hake prey selection is reportedly influenced by seasonal species abundance, it may be expected that fish consumption in St. Georges Bay would increase over the summer, as migrant species populations increase.

Marked differences between male and female diets were found by Waldron (1987) as females were found to consume more fish, and males consumed more crustaceans.

White Hake · *Urophycis tenuis*

White hake, or hake, as they are commonly called in the St. Georges Bay area, are notably a cold water fish that prefer water 5 - 11 ^{O}C, but they are known to travel into warmer shoal areas during the summer (Scott and Scott, 1988). They arrive in the bay in June and appear to favour the mouth of the bay (Kenchington, 1980). This pelagic fish preys heavily upon crustaceans, as well as fish such as herring and gadids.

Published information on white hake diet in the Gulf of St. Lawrence was not found. Data from Bowman and Michaels (1984) for Northwest Atlantic sites are presented in Table 24. Fish comprised on average 88.5 % of the diet, unfortunately, a large proportion of the fish were not identifiable. Those identified included argentines, herring, mackerel, white, red and silver hake, redfish and winter flounder. Bowman et al. (1976) report very similar findings for two sites, but Georges Bank and Gulf of Maine diets were less reliant on fish and more upon crustaceans. Variation in diet between sites is not great, all diets contain a large fish component (43.0 – 88.9 %), gadids being significant in most sites, and sand lance in western Nova Scotia. Arthropods were differentially preyed upon, but in all cases decapod or krill were among the largest prey groups.

Typical diet items for juvenile white hake include calanoid copepods and cladocerons, with an average prey length of 0.74 mm (Coates et al., 1982). In the Bay of Fundy they are reported to feed on amphipods, nematodes, copepods and mysids (Imrie and Daborn, 1981; cited in Scott and Scott, 1988). Bowman and Michaels (1984) found

that more than one half of the young white hake diet in the Northwest Atlantic was of crustaceans; decapod shrimp and krill.

Bowman et al. (1984) found that small white hake of 11 - 15 cm in length consumed polychaetes, amphipods and decapods and that 16 - 20 cm fish preyed upon decapod shrimp (*D. leptocerus, Pandalus borealis),* krill (*M. norvegica)* and mysids. Fish greater than 40 cm ate fish almost exclusively.

Limited information is available on seasonal variation in feeding. Bowman and Michaels (1984) found that white hake fed on various shrimp, mainly *P. borealis* and *M. norvegica* in the spring and fall.

Table 24: Percent weight of prey groups in stomachs of white hake in Northwest Atlantic sites; (1) 1973-1976, Bowman and Michaels (1984) and (2) 1969-1973, Bowman et al. (1976).

	Gulf of Maine 1	S. New England 2	Georges Bank 2	Gulf of Maine 2	W. Nova Scotia 2
Cnidaria	-	-	.	.	.
Annelids	-	**0.2**	**0.1**	**0.2**	**0.1**
Arthropods	**9.3**	**2.6**	**45.5**	**20.0**	**10.7**
Amphipods	.	-	0.1	-	-
Decapods	5.7	2.2	38.8	14.1	4.8
Krill	3.1	-	4.8	5.0	5.1
Isopods	.	-	-	-	0.1
Mysids	.	-	-	-	0.1
Other	0.5	0.4	1.8	0.9	0.6
Molluscs	**0.5**	**7.4**	**7.5**	**0.4**	**0.8**
Gastropods	.	-	**0.1**	-	-
Cephalopods	.	**7.4**	**7.4**	**0.4**	**0.8**
Fish	**88.6**	**88.9**	**43.0**	**76.6**	**86.4**
Herring	1.6	.	.	.	.
Gadids	.	26.6	11.5	1.1	1.3
White hake	20.4	.	.	.	.
Other Gadids	11.5	.	.	.	.
Sand lance	.	-	-	-	5.4
Mackerel	0.7	.	.	.	.
Redfish	0.9	.	.	.	.
Flat Fish	2.6	-	-	3.3	-
Others	44.0	37.9	31.5	49.8	79.7
Miscellaneous	**1.6**	.	.	.	.
Remains	.	**0.9**	**3.9**	**2.8**	**2.0**
No. stomachs	470	79	128	312	91
% empty	31.7	18.4	6.3	12.1	21.9

Pollock · *Pollachius virens*

Among gadids, the pollock is the most inclined towards pelagic existence. Krill constitute the largest proportion of pollock diet in the Bay of Fundy, but fish such as herring, sand lance, silver hake, spotted lanternfishes and silversides contributed more to the diet of pollock in the Laurentian Channel and the Scotian Shelf (Scott and Scott, 1988). The population of pollock in the St. Georges Bay, at the time of an extensive sampling of fish in 1978 was estimated to contribute a negligible biomass to the ecosystem. These fish enter the Bay in the spring, but return to the Gulf of Maine to spawn in the winter (Kenchington, 1980).

Pollock diet in the Northwest Atlantic reported by Bowman et al.(1976) are presented in Table 25. Feeding range is quite narrow, as only 2 groups of crustaceans and fish constitute large prey components. Crustaceans range in composition from 51.1 % – 70.7 %, particularly krill and caridean shrimp, the latter in larger proportions only in the Gulf of Maine. Fish range from 23.6 % to 46.9 % in terms of contribution to the diet, but species are largely unidentified.

Bowman and Michaels (1984) found consistently higher consumption of fish and lower consumption of crustaceans than an earlier study of the diets of these sites by Bowman et al. (1976). Bowman and Michaels (1984) reported that fish comprised 47.2% of the diet and that shrimp contributed 38.8 % to the overall diet of pollock in the Gulf of Maine and western Nova Scotia. Squid was also a component of the diet, contributing 7.7 % when available. Maurer and Bowman (1975) found the relative contribution of

Table 25: Percent weight of prey groups from stomachs of pollock from Northwest Atlantic sites, 1969-1973, Bowman et al. (1976).

	Georges Bank	Gulf of Maine	Western Nova Scotia
Cnidaria	**1.0**	-	-
Annelids	**0.1**	-	**0.1**
Arthropods	**70.7**	**68.7**	**51.1**
Molluscs	**1.7**	**0.1**	-
Gastropods	0.1	-	-
Pteropods	1.6	-	-
Cephalopods	-	**0.1**	-
Tunicates	**0.1**	-	-
Fish	**23.6**	**30.2**	**46.9**
Herring	0.9	3.1	-
Sand lance	-	-	0.6
Gadids	0.5	2.5	1.7
Others	22.2	24.7	44.6
Remains	2.8	1.0	1.8
No. stomachs	197	181	203
% empty	3.6	16.6	22.7

fish and crustaceans to pollock diet reversed, contributing 31.9 % and 65.5 % weight, respectively.

Bowman and Michaels (1984) found that the krill species, *M. norvegica* and *T. inermis*, and the decapod shrimps, *Pasiphaea multidentata, P. borealis* and *D. leptocerus* constituted 60 % of the diet of fish less than 65 cm. Fish was also significant by weight in pollock diet, but constitute a larger proportion of diet for pollock over 65 cm in length. Common fish prey was identified as silver hake, pollock, headlight lanternfishes, mackerel and redfish. No obvious seasonal changes were observed, although fluctuations among squid, juvenile pollock and silver hake compositions of diet occurred. This was attributed to changes in prey abundance.

Young pollock are believed to feed in shallow waters on small crustaceans, particularly amphipods (Scott and Scott, 1988). Bowman et al. (1987), however, found that *M. norvegica* contributed greater than 90 % by weight to the diet of juvenile pollock.

Fourbeard rockling *Enchelyopus cimbrius*

Fourbeard rocklings exhibit a preference for soft muddy bottom. Little is known of their feeding, but they are believed to feed on crustaceans, polychaetes and molluscs (Scott and Scott, 1988). Although they are common to the Southern Gulf, they are usually found at depths greater than 50 m, so may not be prevalent in St. Georges Bay (Kenchington, 1980). Tyler (1972) identified the krill species, *M. norvegica*; the isopod species *Unciola leucopis* and *Maera loveni* and the polychaete *Nephtys incisa* as the major prey of the fourbeard rockling in the Passamaquoddy Bay, New Brunswick.

3. Diet of the benthic community

3.a Benthic Invertebrate Feeding and Diets

Little is known of the benthic invertebrates in the St. Georges Bay area. What is known for the bay and adjacent areas has been summarized (Cameron et al., 2000), and a more general review of benthic communities is in preparation (Mitchell, 2000). In general, polychaetes appear to form a large component of the benthic ecosystem, with molluscs, amphipods, and arthropods also contributing to the biomass and functioning of the system (see Cameron et al., 2000; Mitchell, 2000). However, only a small proportion of these organisms have been well researched for their diet/feeding; though some, such as the lobster, have extensive bodies of information on this facet of their biology. Due to the lack of detailed information on benthic invertebrate species present in St. Georges Bay, coupled with the lack of information on feeding for the vast majority of benthic invertebrate species, the following section reports on the diets/feeding of only 11 taxa - six echinoderms (five sea stars and the green sea urchin) one mollusc species (whelk), and four decapod crustaceans (shore [green] crab, rock crab, snow crab, and American lobster).

ECHINODERMATA

Sea Stars · *Asterias, Crossaster, Solaster, Leptasterias*

Seastars are primarily carnivorous and in the last three decades predation by these animals has been shown to be a major factor in structuring marine benthic communities (Himmelman and Dutil, 1991). Though there are is minimum estimate of seven species of sea stars within the Gulf of St. Lawrence, detailed diet analysis for only five species (*Asterias vulgaris, A. forbesi, Crossaster [Solaster] papposus, Solaster endeca, Leptastarias polaris*) was found in the literature.

Asterias

Himmelman (1991) provides the most complete description of prey for *Asteria vulgaris*, with four mollusc species and a single sea star species forming the majority of the diet of this sea star (Table 26). These results are from the Mingan Islands of coastal Quebec in the northern Gulf of St. Lawrence. Field observations of predation by *A. vulgaris* reported by Himmelman and Hamel (1993) in this same area include the mussel *Mya truncata* (12 of 75 observed predation events), the sand dollar *Echinarchinus parma* (5 of 75 events) and the green sea urchin *Strongylocentrotis droebachiensis* (16 of 75 events). Himmelman and Dutil (1991) provide further data on *A. vulgaris* feeding near these islands, including listing nine taxa observed as prey in the field (Table 27).

Closer to St. Georges Bay, in Lunenberg Bay of southeastern Nova Scotia, Barbeau et al. (1996) report detritus and periwinkles (*Littorina littorea*) forming the

majority of *Asterias* (both *vulgaris* and *forbesi*) diet (17-100% of observed individuals feeding on detritus, 6-59% of observed individuals feeding on periwinkles). These authors also report other prey items at lower frequencies:

- Mussels (*Modiolus modiolus, Mystilus edulis*) 2-24% of observed individuals.
- Scallops (*Placopecten magellanicus*) 4-75% of observed individuals (however, these were only observed on 4 of 19 sample dives, so scallops are thought to be less preyed upon than periwinkles, which were observed being preyed upon 13 of 19 sample dives, despite the initial similarity of figures).
- Slipper shells (*Crepidula fornicata*) 3-12 % of observed individuals.
- Crabs (*Cancer irroratus, Carcinus maenas*) 13 –50 % of individuals (observed on only 5 of 19 sample dives).
- Other sea stars 5-20% of observed individuals) observed on only 2 of 19 sample dives).

Rates of predation of *Asterias* on scallops have been investigated off of Iles-de-la-Madelaine, Quebec by Nadeau and Cliché (1998) and in Lunenburg Bay by Barbeau et al. (1998). Nadeau and Cliché report predation rates of 0.03 to 0.37 scallops/sea star/day. Barbeau et al. report that in laboratory experiments at a density of 80 scallops m^2 the sea star predation rate rarely exceeded 1 scallop/sea star/day. However, this density of scallops is very high and probably unrealistic over most scallop beds. In the range of 0-40 scallops/m^2 these authors indicate predation rates of <0.9 scallops/sea star/day. Results cited by Dickie and Medcof (1963) give a mean rate of only 0.02 scallops/sea star/day (scallop densities not provided).

Crossaster & Solaster

Crossaster papposus (also cited as *Solaster papposus*) is a predator on other sea stars and echinoderms, and unlike other sea star species, also takes cnidarians (Himmelman, 1991; Table 26). Himmelman and Dutil (1991) observed 4 of 10 *C. papposus* preying on the green sea urchin, prey of the remaining six was unidentified. Mauzey et al. (1968) report that of the total observed *C. papposus* in Puget Sound, Washington State, 56% were feeding and of these 50% were eating the pennatulid *Ptilosarcus* and 34% feeding on opisthobranchs *(Hermissenda, Gastropteron, Aglaja diomedea, Melibe leonina)*. Other prey species noted included *Stomphia*, unidentified anaenomes, the barnacle *Balanus crenatus*, *Gastropteron* egg masses, the nudibranch *Dirona albolineata*, the ascidian *Ascidia paratropa*, and the scallop *Chlamys* sp. These authors also cite Mortenson (1927) and Hancock (1958) who report that *C. papposus* is a voracious predator on other sea stars in the British Isles.

At Iles-de-la-Madelaine [Magdalen Islands], Quebec, *C. papposus* was noted to consume 0.05 scallops/sea star/day (Nadeau and Cliché, 1998).

Solaster endeca has a restricted diet compared with other species (Table 26). In addition to those species reported in Table 26, *S. endeca* on the Pacific coast is also

reported to feed upon the sea cucumbers *Cucumaria lubrica* (14 of 21 observations) and *C. miniata* (2 of 21 observations), the ectoproct *Dendrobeania lichenoides* (2 of 21 observations), the holothurian *Thyone benti* (2 of 21 observations), and the ascidian *Corella* sp. (1 of 21 observations) (Mauzy et al., 1968). Himmelman and Dutil (1991) observed only one feeding event by this sea star; it was preying on *Psolus fabrici*.

Leptasterias

Near the Mingan Islands in the northern Gulf of St. Lawrence, *Leptasterias polaris* has a broad diet range including a large number of molluscs, several echinoderms, and ascidians, and a few polychaetes and barnacles (Himmelman, 1991; Table 26). The diet of various sized animals appears to be different, with smaller individuals feeding more heavily on the molluscs *Mytilus edulis* and *Hiatella arctica*, and larger animals feeding on whelks and larger bivalves (Himmelman, 1991). Himmelman and Dutil (1991) at these same islands observed predation on 15 invertebrate taxa (Table 27). Later studies in the same area by Himmelman and Hamel (1993) provided observations on predation by this sea star on benthic invertebrates. Of 108 predation events by *L. polaris* they report observed predation on *Mya truncata* (32 events), the whelk *Buccinum undatum* (12 events), *Spisula polynyma* (11 events), *Ensis directus* (9 events), *Mya arenia* and *Mytilus edulis* (3 events each). Nadeau and Cliché (1998) estimate scallop predation rates of 0.08-0.56 scallops/sea star/day at Iles-de-la-Madelaine, Quebec.

In Puget Sound, Washington State (Mauzey et al., 1968) found that of 154 observed feeding *Leptasterias hexacitis* [a related species] the principle prey were the barnacle *Balanus cariosus* (29% of observations), *Cucumaria lubricia* (23%), *Tonicella* (12%), and *Lacuna* sp. (10%). The remainder of the prey items consisted of *Eupenctata* spp (5%), *Acmaea testudinalis scutulata* (4%) and one each of *L. sitkana, Margarites* sp., *Calliostoma ligatum, Thais lamellosa, Calyptraea fastigatum, Mopalia lignosa, Dodecaceria fistulicola, Mytilus californianus, Chthalamus dalli*, and *Terebratalia tranversa*.

Table 26: Summary of diet of four species of sea stars from Mingan Islands, Quebec, 1981-1982. Numbers represent range of relative frequency (%) of prey in diet as it occurs in 10 cm size classes of sea stars. Table from Himmelman (1991).

	Asteria vulgaris	*Crossaster papposus*	*Solaster endeca*	*Leptasteria polaris*
Mollusca				
Mytilus edulis	0-29	0-1.7	·	0-33.3
Musculus sp.	0-1.4	·	·	0-5.9
Modiolus modiolus	·	·	·	0-2.3
Hiatella arctica	0-28.6	0-1.7	·	0-36.1
Spisula polynyma	·	·	·	0-20
Clinocardium ciliatum	·	0-4.5	·	0-20
Serripes groenlandicus	·	·	·	0-13
Ensis directus	·	·	·	0-4.3
Mya arenia	·	·	·	0-4.7
Mya truncata	0-14.3	0-2.3	·	0-40.0
Macoma sp.	·	·	·	0-2.5
Astarte sp.	·	·	·	0-2.3
Cyrtodaria siliqua	·	·	·	0-4.3
Chlamys islandica	0-50	0-3.3	·	0-8.7
Tonicella marmorea	0-1.4	·	·	0-0.5
Acmaea testidunalis	0-1.4	·	·	0-8.3
Puncturella noachina	·	·	·	0-0.5
Littorina sp.	·	·	·	0-1.0
Lacuna vincta	·	·	·	0-1.0
Margarites spp.	0-1.4	·	·	0-2.8
Buccinum undatum	0-50	0-2.3	·	0-20.0
Aporrhais occidentalis	·	·	·	0-2.3
Echinodermata				
Strongylocentrotus drobachiensis	·	0-47.0		0-2.3
Cucumaria frondosa	·	·	0-18.0	
Psolus fabricii	·	·	0-100	
Psolus phantapus	·	·	0-9.1	
Chridota laevis	·	·	0-9.1	
Echinarachnius parma	0-1.4	0-9.1	0-50	0-2.3
Leptasterias polaris	0-2.8	0-100	0-9.1	
Ophiopholis aculeata	0-33	0-33.3	·	0-0.5
Asterias vulgaris	·	0-33.3	·	
Crossater papposus	·	0-6.8	·	
Hydroids	·	0-10.0	·	
Metridium senile	·	0-2.3	·	
Gersemia rubiformis	·	0-11.0	·	

Table 26 (Con't)

	Asteria vulgaris	*Crossaster papposus*	*Solaster endeca*	*Leptasteria polaris*
Urochordata				
Halocynthia pyriformis	·	·	·	0-2.3
Boltenia ovifera	·	·	·	0-4.7
Ascidia sp.	·	0-1.7	·	0-2.8
Didemnum albidum	·	0-3.3	·	·
Annelida				
Harmothoe sp.	·	·	·	0-0.5
Pectinaria granulata	·	·	·	0-5.6
Potamilla reniformis	·	·	·	0-0.5
Crustacea				
Balanus sp.	·	·	·	0-1.5
Number of individuals observed	276	299	109	1050
Percentage of individuals feeding	29.3	36.1	12.8	29.5

Table 27: Proportion of different prey diets for two sea star species from the Mingan Islands, Quebec, 1984. Range of values represents range of observed predation events at various depths from intertidal to 16 m depth. Table adapted from Himmelman and Dutil (1991).

Prey species	*Asterias vulgaris*	*Leptasterias polaris*
Acmaea testudinalis	0-0.3	0-0.9
Buccinum undatum	·	0-15.4
Littorina sp.	·	0-0.4
Margarites sp.	·	0-0.4
Tonicella sp.	0-6.7	0-1.6
Mytilus edulis	0-99.0	0-73.6
Hiatella arctica	0.5-50.0	0-42.9
Mya truncata	0-6.7	0-40
Mya arenia	·	0-0.4
Macoma spp.	0-10	0-7.7
Clinocardium ciliatum	0-20	0-20
Serripes groenlandica	·	0-7.7
Pectinaria granulata	·	0-0.4
Ophiopholis aculeata	0-0.8	0-1.6
Halocynthia pyriformis	·	0-1.6
Strongylocentrotus droebachiensis	0-0.3	·
Unidentified	0.5-60	20.8-40.0
Total feeding	587	363

Sea Urchin *Strongylocentrotus droebachiensis*

In some areas (i.e., Newfoundland), the green sea urchin is the dominant subtidal benthic animal and they are known to be an important factor in determining the distribution of macrophytes (Himmelman and Steele, 1971; Himmelman, 1980; see also Himmelman, 1984; Himmelman and Nedelec, 1990; Himmelman,1991). They occur throughout the Gulf of St Lawrence and along the Atlantic shore of Nova Scotia, in some locations feeding on the algae to such an extent as to create "urchin barrens" – area in which only a few coralline species of algae can grow. In Nova Scotia an "explosion" of the green sea urchin population through the 1970s (Wharton and Mann, 1981) has resulted in an intense and long standing debate of the roles of the sea urchin, the American lobster (*Homarus americanus*) and various crab and algal species (see for example, Mann and Breen, 1972; Breen and Mann, 1976; Breen, 1980; Elner, 1980; Miller, 1985). Surprisingly, considering the extent of sea urchin grazing of algae and the extent of research on this system, there has been proportionately very little done with respect to sea urchin diets. What has been reported in the primary literature is summarized below.

Field sampling by Himmelman and Steele (1971) in Conception Bay, Newfoundland indicates animals (barnacles, mussels, gastropods) and miscellaneous items (sand, diatoms, detritus, crustose corallines, calcareous chips) are also eaten in addition to algae (Table 28). Laboratory studies by these same researchers indicate urchins will prey upon the sand dollar *Echinarachnius parma*, the sea stars *Asterias vulgaris, Solaster endeca* and *Crossaster papposus*, as well as cannabilize one another when insufficient food is available. Cannibalism is reported from the field as well (Trinity Bay, Newfoundland) (Himmelman and Steele, 1971).

Himmelman (1984) cites other authors as reporting sea urchins absorbing amino acids from the water column (Pearse and Pearse, 1971) and being able to capture zooplankton with their pedicelaria (Leighton and Jones, 1968).

In field experiments at the Mingan Islands, Himmelman and Nedelec (1990) found 18 algal species could be grouped in order of attractiveness to urchins into four homogenous groups.

Group 1: Extremely attractive – *Chordaria, Ulvaria, Alaria*
Group 2: Intermediate attractiveness – *Fucus, Scytosiphon, Laminaria digitata*
Group 3: Slightly attractive – *Spongomorpha, Rhodomela, Saccorhiza*
Group 4: Non-attractive – *Palmaria, Porphyra, Desmarestia, Agarum, Phycodrys, Turnerella, Devaleraea, Ptilota.*

Ascophylum fell between the slightly attractive and non-attractive algae. When the same species were offered individually in the laboratory, however, the classification determined from attractiveness was not correlated with feeding rate (Himmelman and Nedelec, 1990). For example, *Palmaria* was classed as non-attractive yet displayed the

second greatest grazing rate by urchins (Table 29). The most heavily grazed algae were *Rhodomela, Plameria, Spongomorpha, Saccorhiza, Dealeraea,* and *Laminaria digitata.*

Table 28: Frequency of occurrence (%) of diet items found in the green sea urchin in Conception Bay, Newfoundland, 1969. Values represent range of reported frequencies between February and November. Table adapted from Himmelman and Steele (1971).

Food Item	Frequency (%)
Algae	
Phaeophytes[1]	66-100
Corallina officinalis	20-65
Pylaylla littoralis	0-95
Monostroma sp.	0-91
Ulva sp.	0-20
Ptilota serrata	0-38
Animals	
Balanus balanoides	0-70
Mytilus edulis	20-80
Small gastropods[2]	0-50
Miscellaneous[3]	0-100

[1] = fucoids and *Alaria esculenata*
[2] = *Lacuna vincta* and littorinids
[3] = Brown globules of sand, diatoms, detritus, etc. Fragile, white calcareous globules. Hard calcareous chips.

Table 29: Feeding rate (g/urchin/day) of various algal species by sea urchins in the Mingan Islands, Quebec. Table from Himmelman and Nedelec (1990).

Algae	Feeding rate
Rhodomela confervoides	1.22
Palmaria palmata	1.21
Spongomorpha arcta	1.09
Saccorhiza dermatodea	1.07
Devalaraea ramentacea	1.05
Laminaria digitata	1.02
Fucus edantatus	0.9
Chordaria flagelliformis	0.88
Scytosiphon lomentaria	0.84
Ulvaria obscura	0.56
Ascophyllum nodusum	0.5
Alaria esculenta	0.48
Porphyra miniata	0.47
Desmarestia viridis	0.39
Agarum cribrosum	0.34
Ptilota serrata	0.21
Turnerella pennyi	0.06
Phycodrys rubens	0.06

In laboratory experiments green sea urchins fed primarily on algae, preferring *Laminaria longicruris* and *Alaria esculenta* when given selection; the algae *Agarum cribrosum* and *Ptilota serrata* are eaten only when other foods are not available (Himmelman, 1980). Other desirable foods in this research were *Petalonia fascia, Chorda tormentosa*, and H*alosaccion ramentaceum*. Sea urchins of 30 cm test diameter were found to consume, in the laboratory, algae at the following rates; *Laminaria* and *Alaria* approximately 0.6-0.7 g/urchin/day, *Ulva* approximately 0.3 g/urchin/day, *Desmarestia* 0.25 g/urchin/day, *Fucus* 0.2 g/urchin/day, and *Ascophylum, Agarum* and *Ptilota* <0.2g/urchin/day (Himmelman, 1980).

In Maine, USA, green sea urchins were provided a selection of five species of algae in a laboratory experiment. The preferred food ranked as *Laminaria longicruris, Chondrus crispus, Corallina offinalis, Ascophyllym nodusum,* and *Agaraum cribrosum* (Larson et al., 1980). When presented with the five algal species simultaneously, consumption rates were 0.35-0.46 g/urchin/day for *Laminaria*, 0.11-0.28 g/urchin/day for *Chondrus*, 0.09-0.14 g/urchin/day for C*orallina*, 0.04-0.05 g/urchin/day for *Ascophyllum*, and 0.04 g/urchin/day for *Agarum*. The feeding rate on all algae varied seasonally with the lowest values occurring in January and February (Larson et al., 1980). Himmelman (1980) also found consumption rates low in February then increased to high values by May.

MOLLUSCA

Whelks · *Buccinum undatum*

The whelk is the most common invertebrate predator in the northern Gulf of St. Lawrence occuring at densities up to 1.82 individuals/m^2 (Himmelman, 1991; Himmelman and Hamel, 1993) and has been found in Northumberland Strait adjacent to St. Georges Bay (Caddy et al., 1977). Of 16 observed feeding events by the whelk near the Mingan Islands, Quebec, 12 were on the clams *Mya truncata, Clinocardium ciliatum, Serripes groenlandica,* and *Spisula polynyma* and 4 were on the toad crab *Hyas araneus* (Himmelman, 1991). The whelks are not thought to have killed the crabs but rather found them by scavenging. In an examination of whelk stomach contents, Himmelman and Hamel (1993) suggest that the relatively low proportion of individuals with food in their stomachs (57%), and the difficulty of identifying remains imply a diet of soft bodied animals (i.e., few hard parts remain for identification). They also suggest that these animals feed by three strategies. 1) active predation, 2) scavenging, and 3) associating with sea stars in order to pick up debris and leftover from the sea star feeding activities. Of 200 stomachs examined, these researchers found only 30 stomachs with identifiable prey items, these included Oligochaetes (1 stomach), Polychaetes (7 stomachs), bivalves (1 stomach), Amphipods (3 stomachs), Decapods (9 stomachs), insect larvae (1 stomach), sea urchin remains (5 stomachs), and fish eggs (3 stomachs).

Green [Shore] Crab · *Carcinus maenas*

Green crabs were introduced accidentally from the eastern Atlantic and is found along the eastern coast of Canada and United States (Holthius and Gottlieb, 1958). They are a non-commercial species, but are of interest as potential competitors with native crab species.

Green crabs were collected from Port Hebert, southwestern Nova Scotia and analyzed by Elner (1981). He reports that 80% of 762 crabs had food in their stomachs with molluscs, particularly bivalves, and of these *Mytilus edulis* and *Mya arenaria*, being the most important food items. Table 30 provides approximate frequency of occurrence of food in stomachs; values are interpreted from figures presented in Elner (1981) and so are approximations only. Cannibalism by the green crab appears to occur.

Thirty one kinds of food were identified in 3,979 green crab stomachs off New Hampshire and Massachussets in 1954-56 by Ropes (1968) (Table 31). Thirty three percent of these 3,979 stomachs contained plants while 88% contained animals. Preferred food items from this study are presented in Table 32. In addition to these listed items, Ropes (1968) also reports *Anomia* sp., *Aquipecten irradians*, and *Zostera marina* in other crabs outside of his study area. He also cites Spear (1955) reporting green crabs eating the hard clam *Mercenaria mercenaria* in the laboratory, and Dearborn (1957) who found acceptable foods to the green crab include *Crassostrae virginica, Astarte castanea, Placopecten magellanicus, Nucula* sp., *Modiolus modiolus, Callocardia morrhuana, Spisula solidissima, Hiatella arctica, Fundulus* sp., *Laminaria* sp., *Littorina littorea* and *L. obtusata.*

In a laboratory experiment exposing the green crab to various densities of the mussel *Mytilus edulis*, Elner and Hughes (1978) found that at simulated low densities (equivalent to 20-80 mussels/m^2) crab predation rate was approximatelly 11 mussels/crab/day. At medium densities (equivalent to 100-400 mussels/m^2) predation rate was close to 28 mussels/crab/day, and at high densities (equivalent to 200-800 mussels/m^2) predation rate was approximately 23 mussels/crab/day. In a second experiment, holding the prey density constant at the equivalent of 1,000 mussels/m^2 but of varying prey sizes, predation rate was seen to range from 19.47 to 22.34 mussels/crab/day. MacKenzie (1977) reports Connecticut rock crabs consuming 100 clams *(Mercenaria mercenaria)* per day in laboratory experiments and for short periods would consume up to 30 clams/hour.

Table 30: Percentage frequency of occurrence (%) of food types in the food containing stomachs of 762 green crabs from Port Hebert, Nova Scotia, for two periods in 1978. Data from Elner (1981)

Prey type	May (1978)	August (1978)
Animal	86	85
Mollusc (total)	74	81
Bivalve	74	81
Gastropod	21	43
Mytilus edulis	41	59
Mya arenia	47	75
Crustacea[1]	4	18
Other[2]	6	9
Unidentified	23	21
Algae	27	52
Brown	6	52
Green	19	4
Sediment	6	21
Unidentified	2	6

[1] = includes *Cancer irroratus*, *Carcinus maenas*, barnacles, amphipods, isopods, hermit crabs.
[2] = includes colonial hydroids, bryozoans, unidentified eggs, polychaetes (*Nereis*), and echinoderms (*Strongylocentrotus drobachiensis*, *Asterias vulgaris*)

Table 31: List of prey items in stomachs of 3,979 green crabs collected in New Hampshire and Massachusetts, 1954-56. From Ropes (1968)

Annelids	**Gastropod mollusc**	**Barnacles**
Nereis sp.	*Littorina* sp.	*Balanus* sp.
Glycera sp.	*Polineces* sp.	
Clymenella sp.	*Odostomia* sp.	**Other animals**
	Hydrobia minuta	Foraminifera
Pelycypod mollusc		Colonial hydroids
Solemya velum	**Arthropods**	Insects
Mytilus edulis	Crabs	Fish
Modiolus demissus	*Pagurus* sp.	
Mysella planulata	*Cancer irroratus*	**Plants**
Gemma gemma	*Carcinus maenas*	Algae
Petricola pholadiformis	*Limulus polyphemus*	*Spartina* sp.
Tellina sp.		
Macoma sp.	Small arthropods	
Ensis directus	*Isopods*	
Mya arenia	*Amphipods*	
	Natantia	

Table 32: Percent frequency (%) of food items in 3,979 green crab stomachs in New Hampshire and Massachussets, 1954-56. Data from Ropes (1968).

Food item	Percent frequency
Animals	87
Annelids	8
Nereis sp.	5
Molluscs	75
Pelecypods	68
Mytilus edulis	44
Mya arenia	28
Gemma gemma	24
Other pelecypods	23
Gastropods	26
Hydrobia minuta	11
Other gastropods	3
Arthropods	27
Crabs	11
Small arthropods	9
Barnacles	4
Fish	2
Foraminifera	2
Insects	1
Other animals	1
Plants	31
Algae	13
Spartina sp.	26
Unidentified	74
Stomachs with food	63

Snow Crab *Chionoecetes opilio*

The snow crab is the predominant epifaunal invertebrate at shelf depths in the North Atlantic (Lovrich and Saint-Marie, 1997) and is the most important commercial crab species in Atlantic Canada (Wieczorek and Hooper, 1995). They occur most commonly on muddy or sand-mud bottoms and, off Cape Breton, are typically found at depths between 5 and 245 m (Anonymous, 1990).

In an analysis of 107 snow crab stomachs from the Magdalen Shallows, Powles (1968) reports mollusc fragments (probably *Yoldia* sp.) being the most frequent prey item with amphipods also making up a significant proportion of the diet (Table 33). Wieczorek and Hooper (1995) report that in Bonne Bay, Newfoundland, snow crabs appear to scavenge feed on dead fish and to cannabalize each other, but their primary prey consist of bottom invertebrates, often species with low mobility. Of 498 crabs

stomachs examined, the most frequent food types were plant matter (35.9% occurrence), fish (32.7%), annelids (30.9%), crustaceans (23.7%), molluscs (18.1%) and echinoderms (15.7%). Table 34 summarizes their results from Bonne Bay.

Sampling by Lefebvre and Brethes (1991) indicated the diet is dominated by crustacea (85% of stomachs), followed by polychaeta (83%) and mollusca (19%), at Baie des Chaleurs, Gulf of St. Lawrence (Table 35). Cannibalism appears to be relatively common. Lovrich and Saint-Marie (1997) found cannibalism rates of 7.2% but as high as 10-22% in Baie Saint-Margarite, northwestern Gulf of St. Lawrence, while Powles (1968) reported cannibalism rate of 8% for Baie des Chaleurs, and Wieczorek and Hooper (1995) found cannibalism rates in Bonne Bay Newfoundland of 1.6 to 4.5%.

In comparison with the presence of food items in the environment, Wieczorek and Hooper (1995) suggest that errant burrowing polychaetes, small gastropods, amphipods and holothurians are selected against (i.e., not a preferred food item). Porifera, *Yoldia* spp., *Ophiura* spp. and small crustaceans appear to be a preferred food. Other items appear to be eaten roughly in proportion to their abundance in the environment. These authors also cite another study (Brethes et al., 1982) which found polychaetes to be the least selected food group, and echinoderms most preferred followed by molluscs and crustaceans. In addition, Lovrich and Saint-Marie (1997) report that stomach contents change as the crab matures. For example, adult males of carapace width of >60 mm contained more fish and unidentified food items, and less echinoderms, than adult males of 40-50 mm carapace width.

Table 33: Number of stomachs in which a food item was present in 107 snow crab stomachs from the Magdalen Shallows, Gulf of St. Lawrence. Table from Powles, 1968.

Food item	Number of stomachs
Polychaete	
Sedentary	20
Errant	1
Unclassified	45
Mollusc	
Yoldia sp.	80
Other pelycypod	11
Gastropod	10
Crustacean	
Amphipod	35
Chionoecetes opilio	9
Echinoderm	
Ophiuroid	36
Vertebrate	13
Eggs	11
Empty	4

Table 34: Percentage frequency of occurrence of 498 snow crab stomachs from Bonne Bay, Newfoundland, 1990. Percentage frequency represents range of values observed from five locations within the bay. Table modified from Wieczorek and Hooper, 1995.

Food type	Percentage frequency
Annelida	12.6-40.5
Sedentary polychaetes	6-26.4
Errant polychaetes (surface dwelling)	2.5-10.6
Errant polychaetes (burrowing)	0.5-3.8
Echinodermata	00.8-31.2
Ophiur spp.	0.8-29.6
Strongylocentrotus drobachiensis	0-2.5
Holothuridae	0-1.7
Mollusca	3.3-22.4
Bivalves (Nuculanidae, Cardidae, Mytilidae, Mallayidae, unidentified))	0.8-19.4
Bivalves (*Nuculans tenuisculcata, Nuculla* sp. *Crenella faba*)	0.5-11.9
Yoldia sp.	0.3-5.2
Cerastoderma spp.	0-1.5
Gastropods (Buccinidae, Lacunidae, Trochidae, unidentified)	1.5-9.1
Gastropods (*Lacuna* sp., *Margarites* sp., *Lora* sp.	1.5-4.6
Crustacea	19.3-27.2
Chionoecets opilio	1.6-4.5
Hyas sp.	0-1.6
Natantia	5.0-18.2
Amphipoda	0.8-5.0
Small crustaceans	4.5-9.9
Cnidaria	0.8-24.8
Porifera	6.4-22.3
Bryozoa	0.8-9.9
Foraminifera	0-5.0
Fish	23.5-50.7
Plant material	12.8-62.8
Non-food (sediment, plastic, rubber, metal)	15.2-35.8
Unidentified	4.5-13.4

Table 35: Percentage frequency of occurrence of 650 snow crab stomachs from baie desvChaleurs, Gulf of St. Lawrence, 1986-87. Table from Lefebvre and Brethes (1991).

Stomach content	Percent frequency
Polychaeta (Total)	83.1
Polynoidae	48.3
Sigalionidae	32.3
Nephtydae	29.2
Phyllodocidae	21.2
Nereidae	0.5
Hesionidae	4.8
Glyceridae	1.2
Sphaerodoridae	0.2
Lumbrineridae	15.5
Capitellidae	2.8
Dorvilleidae	0.3
Spionidae	32/6
Maldanidae	19.2
Flabelligeridae	6.9
Scalibrgemidae	1.7
Trochochetidae	0.8
Terebellidae	1.7
Sabellidae	2.9
Pectinaridae	0.2
Serpulidae	1.7
Ampharetidae	0.8
Sternaspididae	0.2
Unidentified	22.8
Crustacea (Total)	85.1
Decapoda	0.5
Tanaidacea	2.2
Cumacea	10.2
Euphausicea	25.5
Amphipoda	18.0
Copepoda	16.9
Isopoda	0.2
Unidentified	43.6
Mollusca (Total)	18.8
Pelycypoda	3.8
Gastropoda	8.8
Unidentified	7.2
Sponge spicules	36.8

Rock Crab · *Cancer irroratus*

The rock crab is a non-commercial crab species occurring within similar habitats as the commercially important lobster, though they may utilize the available habitat in different ways (e.g.,crabs will bury themselves, while lobsters excavate burrows) (Scarrat and Lowe, 1972). It is known to be present in the St. Georges Bay area, and in the Northumberland Strait it has been associated with areas predominately composed of boulders, sand or mud (Scarrat and Lowe, 1972).

Rock crabs consume a large variety of foods (Tables 36 and 37). In Northumberland Strait, near Richibucto, New Brunswick, Scarrat and Lowe (1972) indicate principle prey species of the rock crab as nereid and polynoid polychaetes, the mussel *Modiolus modiolus*, the sea star *Asterias vulgaris* and the green sea urchin. Near the Isle-de-la-Madelaine principle identifiable food items were found to include *M. modiolus*, ectoprocts, polychaetes and algae (Hudon and Lamarche, 1989). In addition, this latter study found lobster (*Homarus americanus*) within rock crab stomachs, indicating that large crabs may prey upon smaller lobsters. This is in contrast to many other reports that maintain that crabs do not eat lobsters, though lobsters readily prey upon crabs. In a small sample (100 crabs of which 57 had food in them) from West Dover on the Atlantic coast of Nova Scotia, Drummond-Davis et al. (1982) list 13 food items of which the hermit crab *Pagurus* forms the predominant portion of the diet (present in 26% of the stomachs). Polychaetes were present in four stomachs, crustaceans and sea urchins each in two stomachs, and periwinkles and mussel byssal thread each in one crab stomach. Algae (five stomachs) and *Zostera* (three stomachs) were also present.

A laboratory experiment of food preference by the rock crab conducted by Drummond-Davis et al. (1982) at West Dover, Nova Scotia, indicates that mussels (*Mytilus edulis*) are preferred over green sea urchins which in turn are preferred over the sea star *Asterias vulgaris*. Consumption rates reported by these authors range from 2.3 to 5.0 mussels/crab/day, and 0-1.3 urchins/crab/day. No starfish were eaten when they were offered with urchins available. Elner (1980), in laboratory experiments using rock crabs from Passemequoddy Bay, New Brunswick, also found that the mussels *Modiolus modiolus* and *Mytilus edulis* were preferred over sea urchins. When sea urchins were the only available prey rock crabs were found to feed on them at rates of approximately 0.6 to 1.8 urchins/crab/day (though one trial indicated as high as 3.5 urchins/crab/day; Figure 4 in Elner, 1980). Himmelman and Steele (1971) report a range of 0.6 to 2.2 urchins/crab/day. When presented with a combination of mussels and urchins, rate of consumption of urchins dropped to 0.09 urchins/crab/day and mussel consumption was 7.11 mussels/crab/day; mussels were selected by a ratio of 79:1 when both were presented in equal availability (Elner, 1980). However, these values should be interpreted with caution, as Garnick (1978) indicates that the rate of sea urchin predation in the field may be lower than that observed in the laboratory due to the formation of defensive aggregations by the urchins.

Table 36: Percentage (%) frequency of occurrence in stomachs of 230 rock crabs from Northumberland Strait, 1967. Table modified from Scarrat and Lowe (1972).

Food item	June, 1967	Sept.-Oct. 1967
Animal		
Foraminifera	0.5	·
Porifera	1.5	·
Tunicata	1.5	3.6
Amphipoda	2.5	3.6
Isopoda	0.5	·
Polychaeta	19.3	17.8
Chiton	0.5	7.1
Pelycypoda	2.0	3.6
Gastropoda	1.5	3.6
Modiolus modiolus	3.0	32.2
Turbellaria	·	3.6
Cumacea	1.0	·
Asterias	1.0	14.3
Stongylocentrtus droebachiensis	4.0	10.7
Cancer irroratus shell	·	3.6
Shell fragments	15.3	17.8
Plant		
Rhodophyceae	1.5	·
Zostera	4.4	·
Miscellaneous		
Sand	10.4	·
Amorphous matter	35.1	82.1
Liquid	17.8	35.7
Total examined	202	28
Empty	59	·

Table 37: Food item in 239 rock crab stomachs from Isle-de-la-Madelaine, 1985. Values are average abundance score (e.g., 1 indicates present as less than 10% of total stomach volume, 2 is between 10-20%, etc.). Table from Hudon and Lamarche (1989).

Food item	Gros Cap	Cap Irving
Foraminifera	0.219	0.067
Porifera	·	0.01
Hydroida	0.082	0.029
Ectoprocta	1.534	0.086
Prosobranchiata	0.014	0.029
Lacuna vincta	0.274	0.181
Margarites sp.	·	0.019
Pelycypoda	0.219	0.105
Mytilidae	0.014	0.038
Modiolus modiolus	4.466	2.114
Tellina agilis	0.014	0.086
Polychaeta	·	0.01
Nereidae	0.288	0.143
Polynoidea	0.027	0.21
Lepidinotus squamatus	·	0.81
Harmothoe sp.	·	0.019
Terebellidae	0.151	1.038
Glyceridae	·	0.048
Crustacea	0.014	0.01
Ostracoda	0.014	0.019
Copepoda	0.014	0.019
Isopoda	0.055	0.038
Amphipoda	·	0.01
Gammarus sp.	·	0.133
Ischyocerus sp.	0.055	0.019
Psammonyx nobilis	·	0.010
Corophium sp.	0.027	0.029
Jassa falcata	0.041	·
Monoculodes sp.	0.014	·
Acarina	0.014	·
Cirrepedia (*Balanus* sp.)	·	0.086
Decapoda	0.192	0.219
Homarus sp.	·	0.21
Cancer sp.	0.192	0.305
Strongylocentrotus	0.137	0.01
Fish	·	0.343
Flesh	·	0.076
Flocculent matter	1.041	3.172
Algae	1.0	0.590
Nylon	·	0.01
Unidentified	0.055	0.152

Laboratory feeding experiments of rock crab predation on the sea scallop (*Placopecten magellanicus*) at Iles-de-la-Madelaine indicate mean predation rates on the bivalve of 1.02 to 4.22 scallops/crab/day, though as many as 12 scallops/crab/day were recorded (Nadeau and Cliché, 1998). Rock crabs from the Passamequoddy Bay area were found to have mean predation rates on scallops in the laboratory of 4.14 to 7.29 scallops/crab/day with a daily range from 0 to 11 scallops/crab/day (Elner and Jamieson, 1979). Predation rates of up to approximately 14 scallops/crab/day at high scallop densities were found in a field study in Lunenburg Bay and the authors suggest that, based on this and previous laboratory experiments, an estimated predation rate of 10 scallops/crab/day at high scallop densities is reasonable (Barbeau et al., 1998).

Rock crabs also feed on the American oyster (*Crassotrea virginica*) and have been reported to prey on these bivalves at mean rates of 4.5 oysters/crab/day in the laboratory (Elner and Lavoie, 1983). Small oysters (2-9 mm shell length) on chinese-hat spat collectors were found to be consumed at much lower rates though, from 0.34 to 3.12 oysters/crab/day.

American Lobster · *Homarus americanus*

Lobster has been, and continues to be, an extremely important fishery in the St. Georges Bay area. Most of the research within this area, however, has been on growth, survival and distribution of these crustaceans; little appears to have been done on diets or feeding. In contrast, there has been considerable research conducted on stomach contents and feeding preferences by the lobster in other areas of Atlantic Canada. Much of this has been spurred by the hypothesis that the lobster may be a keystone species in kelp beds and may have been significant in keeping the green sea urchin population in check prior to the 1970s (see Mann and Breen, 1972; Breen and Mann, 1976; Breen, 1980). Although this hypothesis has not been substantially supported by data (Miller, 1985), it did serve as a catalyst and focal point for a substantial amount of research on the interactions of the lobster and its environment within the Gulf of St. Lawrence and Atlantic Nova Scotia. The principle papers and results are summarized below.

Larval Lobster

The diet of larval lobster within St. Georges Bay are reported by Harding et al. (1983). Stage I larvae feed on the zooplanters *Podon, Temora* (Stages IV, V, and adults), *Acartia* (Stage V and adults), *Pseudocalanus* (Stage V) and *Centropages* (Stage V) while the final two stages of larval lobster development prey preferentially on adult female *Centropages*, large gastropod larve, and the zoea and megalops larvae of the rock crab (Table 38; see also Cameron et al., 2000 for overview of St. Georges Bay zooplankton)

Immature Lobster

Hudon and Lamarche (1989) state that immature lobsters have a similar diet to adults although the proportions of food items may differ. Carter and Steele (1982a) report at least 33 taxa of organisms observed in the stomachs of immature lobsters captured in Placentia Bay, Newfoundland (Table 39). No immature lobster stomachs were empty (this is in contrast to most diet studies where a significant proportion of stomachs are empty) and the estimated percentage contributions to the contents were decapod crustaceans (26.7%), molluscs (19.9%), echinoderms (19%), miscellaneous (14.7%), polychaetes (10.9%) and amorphous material (8.8%).

Table 38: Average frequency of prey type/larval lobster from St. Georges Bay, 1979. Table from Harding et al. (1983).

		Lobster Larvae			
Gut content	prey item stage	Stage I	Stage II	Stage III	Stage IV
Amorphous material		0.1	·	·	·
Temora	IV	0.1	0.1	0.5	·
Pseudocalanus	V	0.1	·	·	·
Acartia	V	0.2	0.2	0.5	·
Acartia	VI (female)	0.1	·	0.5	·
Pseudocalanus	VI (female)	·	0.1	·	·
Centropages	V	0.2	0.1	0.5	0.2
Temora	VI (male)	0.1	0.2	0.5	0.1
Temora	V	0.6	1.0	1.5	0.3
Temora	VI (female)	0.5	2.4	1.5	0.1
Gastropod larvae		·	0.1	·	0.6
Podon		1.3	1.5	3.5	0.5
Centropages	VI (male)	·	0.1	·	·
Centropages	VI (female)	·	0.2	1.0	0.7
Tortanus	VI (male)	·	·	·	0.1
Tortanus	VI (female)	·	·	·	0.1
Fish eggs		·	·	·	0.1
Calanus	IV	·	·	·	0.1
Calanus	V	·	·	·	0.1
Cancer	Zoea	·	·	1.0	·
Cancer	Megalops	·	·	·	0.8
Insect pieces		·	·	0.5	0.3
Sample size (n)		21	14	2	16

In a laboratory study of the attraction of various prey species to immature lobsters from Placentia Bay, Newfoundland, Carter and Steele (1982b) found that the brittlestar *Ophiopholia aculeata* was attacked in 78.3% of trials, nereid and polynoid polychaetes

75 and 71.4% respectively, rock crabs 65.6%, seastars (*Asterias vulgaris*) 61.5%, mussels (*Mytilus edulis*) 48.6%, sea urchins 32.4% and periwinkles 0%. Thus, immature lobsters appear to indicate a food preference for polychaetes and rock crabs over sea urchins and periwinkles. A mean maximum possible prey consumption (thought by authors to be an over estimate) by immature lobsters of 4.69% of lobster body weight was estimated for these predator-prey interactions.

Adult Lobster

In a historical review of lobster feeding research, Scarrat (1980) cites Herrick (1909) as reporting the food of lobsters consisting principally of fish, benthic invertebrates (isopods, decapods, molluscs, seastars, sea urchins and hydroids), algae, eelgrass, shell fragments, sand and gravel. Dow (1949) stated that from observations on lobsters in captivity and the experience of commercial fishermen it was believed that lobsters ate fish, molluscs and other invertebrates, and small quantites of algae.

At Iles-de-la-Madelaine, of 175 lobster stomachs, the five most abundant prey species for adult lobster were found to be (in decreasing order) the mussel *Modiolus modiolus*, lobster, rock crabs, the mollusc *Lacuna vincta*, and ectoprocts (Hudon and Lamarche, 1989). Table 40 provides data on adult lobster stomach contents at this location. Unpublished results from near Prince Edward Island by Scarrat (cited by Miller et al., 1971) include frequency of occurrence of mussels (67%), rock crabs (50%), polychaetes (42%), periwinkles (36%), sea urchins (23%) and sea stars (5%).

At Kouchibouquac Bay [Northumberland Strait], New Brunswick, lobster stomachs were found to contain principally eelgrass (*Zostera*), polychaetes (nerieds, polynoids, and polydorids), rock crabs, lobster (presumed to be molted exoskeletons), mussels (*Modiolus modiolus*), *Asterias vulgaris*, sea urchins and tunicates (primarily *Molgula* sp.) (Scarrat, 1980). Table 41 provides a range of percentage frequency of occurrence of stomach contents for lobsters from the Kouchibouquac Bay area between 1965 and 1967.

Ennis (1973) found that in Bonavista Bay, Newfoundland, of 288 stomachs examined, the toad crab *Hyas araneus* and the rock crab *Cancer irroratus* were the main foods of the lobster, making up almost half of the total food consumed (Table 42). The sea urchin (7.1%), several mollusc species (10.9%), and several sea star species (10%) made up the bulk of the remainder of the stomach contents. Near Newfoundland, Squires (1970) found the frequency of occurrence of the principle prey of 186 trap caught lobsters to consist of fish (50%; thought to be bait), polychaetes (37%), rock crab (27%), periwinkles (22%), sea urchins (4%), mussels (4%), sea stars (3%) and brittle stars (1%). A lobster taken from 95 fathoms off of St. John's, Newfoundland was found to contain fragments of the toad crab *Hyas*, snow crab *Chionoecetes*, the whelk *Neptunea*, gastropods, small fish bones and pieces of the seaweed *Ptilota* (Squires and Ennis, 1968).

Table 39: Percent frequency of occurrence (%) of food items in stomachs of 103 immature lobsters from Placentia Bay, Newfoundland, 1976. Table modified from Carter and Steele (1982a).

Stomach item	June-mid August	Late August-mid September	October-November	Total
Echinoderms				
Sea urchin	73.9	87.5	57.6	71.8
Brittle star	26.1	50.0	33.3	34.0
Starfish	6.5	-	9.1	5.8
Molluscs				
Mussels	50.0	75.0	81.8	66.0
Periwinkle	8.7	58.3	42.4	31.1
Chiton	15.2	45.8	15.2	22.3
Cockle	17.4	16.7	15.2	16.5
Limpet	17.4	12.5	-	10.7
Bivalves & Gastropods[1]	<13.0	<16.7	<3.0	<9.7
Unidentified bivalves	6.5	45.8	18.2	17.5
Unidentified gastropods	15.2	29.2	12.1	19.4
Decapod crustaceans				
Rock crab	28.3	91.7	60.6	53.4
Lobster	8.7	50.0	-	15.5
Hermit & toad crab	4.3	-	<3.0	<2.9
Unidentified crustacean	21.7	8.3	15.2	16.5
Polychaetes				
Polynoids	28.3	91.7	42.4	47.6
Nereids	34.8	62.5	30.3	39.8
Unidentified polychaetes	15.2	4.2	18.2	13.6
Algae				
Filamentous	56.5	12.5	12.1	32.0
Miscellaneous	<4.3	4.2	<3.0	<2.9
Miscellaneous				
Pelagic copepods	34.8	12.5	33.3	29.1
Hydrozoans	19.6	16.7	33.3	23.3
Bryozoans	19.6	8.3	-	10.7
Unidentified fish	4.3	4.2	-	2.9
Miscellaneous invertebrates[2]	<6.5	-	<3.0	<2.9
Pebbles & sand	78.3	37.5	36.4	55.3
Wood fibres	23.9	12.5	24.2	21.4
Tissue bolus	17.4	8.3	18.2	15.5
Rubber	2.2	20.8	6.1	7.8
Plastic	2.2	-	-	1.0
Amorphous material	97.8	100	87.9	95.1
Sample size (n)	46	24	33	103

[1] = *Buccinum undatum, Lacuna vincta, Lora biocominata, Margarites costalis, Anomia aculeata, Hiatella arctica, Musculus discors, Tellina agilis.*

[2] = Unidentified sponge, unidentified amphipod, unidentified isopod, nauplius larva.

In the most comprehensive listing of lobter diets, 65 prey taxa were found in 1,032 lobster stomachs sampled from Lobster Bay, southwestern Nova Scotia by Elner and Campbell (1987) during a comparison of lobster diets from macroalgal communities and urchin barrens (Table 43). The mussels *Mytilus edulis* and *Modiolous modiolus* were consistently one of the most important diet items in both environments. Other important prey items included bivalves, ascidians, crabs, hermit crabs, gastropods and lobsters at the macroalgal site, and sea urchins, polychaetes, gastropods, pebbles/foreign material, chitons, algae and shrimp-like crustaceans within the urchin barrens. The diet was of greater diversity at the macroalgal site as compared to the barrens.

Changes in the diet of lobsters with location and season (Ennis, 1973), and size and molt cycle (Scarrat, 1980) are apparent, making generalizations of diet tenuous. For example, polychaetes are more abundant in the stomachs of larger lobsters, and lobster shell, chitons and mollusc fragments (calcium-rich foods) form larger proportions of the diet soon after moulting than decline as the skeleton hardens (Scarrat, 1980).

In a field experiment using enclosures in Northumberland Strait in 1979 Jamieson et al. (1982) found that the horse mussel *Modiolus modiolus* was preferred when offered a choice of it or the sea scallop *Placopecten magellanicus*. The order of preference was mussel, then other lobsters (cannibalism) and lastly sea scallops. In a second study reported in the same paper, in St. Margarets Bay, Nova Scotia, lobsters placed in an enclosure with the prey species, horse mussels, sea scallops, rock crabs (*Cancer irroratus*) and shore crabs (*Carcinus maenas*) only the mussels and scallops were eaten. This appears to indicate a feeding preference for these two species over the crabs present.

In the laboratory, lobsters from southeastern Nova Scotia have been shown to prefer rock crabs to sea urchins by a factor of 5:1 at density ratios of 0.25 crab per urchin up to 8 crabs per urchin (Evans and Mann, 1977). At high densities of urchins relative to crabs (8:1 to 100:1) the ratio consumed by lobsters remains relatively constant at approximately two urchins for one crab. At and below a density of two urchins per crab in the aquarium, the number of urchins eaten per crab were less than 0.8, and at 4 urchins per crab there was roughly one urchin eaten for each crab (Evans and Mann, 1977). This suggest that the lobsters are preferentially feeding on rock crabs over sea urchins.

Experiments using starved lobsters from Passamoquoddy Bay, New Brunswick, resulted in only 39% of the lobsters feeding on sea urchins in a six day period (total of eight days without food) when they were presented as the only food source (Elner, 1980). When sea urchins were offered with mussels (*Mytilus edulis* and *Modiolus modiolus*) lobsters displayed an overwhelming preference for mussels (0.18 urchins/lobster/day and 7.82 mussels/lobster/day; ratio of urchins to mussels consumed 1:43.4) (Elner, 1980). Under conditions of unlimited urchin availability, mean lobster consumption was only about one urchin/lobster/day. Himmelman and Steele (1971), using lobsters and urchins from Conception Bay, Newfoundland, report a laboratory mean consumption rate of 0.3 urchins/lobster/day and a maximum rate of 1.2 urchins/lobster/day.

Miller (1985) summarized available data on sea urchin predation by lobsters. His Table 1 is condensed and summarized in Table 44.

Laboratory experiments of Passamaquoddy Bay lobsters feeding on sea scallops (*Placopecten magellanicus*) indicated mean daily feeding rates from 3.0 to 10.14 scallops/lobster/day, with an overall mean value of 6.07 scallops/lobster/day (Elner and Jamieson, 1979). In tests using lobsters from this same area on the American oyster (*Crassostrea virginica*), mean maximum predation rates were 28 oysters/lobster/day, and mean consumption rate was found to range between approximatelly 3-15 oysters/lobster/day for lobsters<80 mm carapace length, and from 6-28 oysters/lobster/day for lobsters 80-110 mm carapace length (Elner and Lavoie, 1983).

The considerable research on lobster feeding had led to the question of whether these animals are simply opportunistic feeders, taking whatever is available, or they actively select certain items over others. Hudon and Lamarche (1989) suggest that lobsters are opportunistic, as their diet reflects local and seasonal availability of food items, and Elner and Jamieson (1979) agree that the animals' diets largely reflect the relative abundance of prey species available in their immediate habitat. Scarrat (1980) concludes that lobsters are most unspecialized feeders, consuming almost anything, yet their feeding is not entirely random and there is some selection of food items. Based on their results and previous studies Elner and Campbell (1987) suggest that lobsters are selective feeders with a complex foraging behaviour that is capable of maintaining gross diet composition despite sharp variation in prey availability. For the author Elner this is in contradiction with his 1979 findings with Jamieson. Finally, with the caveat that if a derived index of hard parts reflects selection for the whole organism, Carter and Steele (1982a) report that their field study indicates that rates of consumption of prey are not proportional to the natural availability of prey species. Obviously, the matter of lobster food selectivity is far from resolved.

Table 40: Food item in 175 lobster stomachs from Isle-de-la-Madelaine, 1985. Values are average abundance score (e.g., 1 indicates present as less than 10% of total stomach volume, 2 is between 10-20%, etc.). Table from Hudon and Lamarch (1989).

Food item	Gros Cap	Cap Irving
Foraminifera	0.026	0.143
Hydroida	0.155	0.405
Ectoprocta	0.371	0.357
Prosobranchiata	0.052	0.167
Lacuna vincta	0.698	0.357
Margarites sp.		0.071
Nassarius sp.	0.052	
Polinices immaculatus	0.017	
Pelycypoda	0.155	0.214
Mytilidae	0.06	
Modiolus modiolus	2.422	1.571
Tellina agilis	0.069	0.119
Polychaeta	0.026	
Nereidae	0.147	0.143
Polynoidea	0.069	0.119
Lepidinotus squamatus	0.052	0.381
Terebellidae		0.048
Spirobis sp.		0.024
Crustacea	0.009	
Copepoda	0.043	
Isopoda	0.017	
Amphipoda	0.026	
Ischyocerus sp.	0.078	
Corophium sp.	0.009	
Jassa falcata	0.043	
Caprelloidea	0.009	
Acarina	0.009	
Cirrepedia (*Balanus* sp.)	0.103	0.143
Decapoda	0.267	0.310
Caridea		0.024
Pagurus sp.	0.009	
Homarus sp.	1.759	1.69
Cancer sp.	1.681	0.405
Echinodermata		0.024
Asteroidea	0.216	
Ophiuroidea		0.048
Strongylocentrotus	0.328	0.238
Ascidiacea	0.095	0.048
Fish	0.086	0.071
Flesh	0.172	0.048
Flocculent matter	3.112	3.523
Algae	0.621	1.571
Corallina officinalis	0.009	0.024
Nylon	0.026	0.024
Unidentified	0.103	0.214

Table 41: Range of percentage frequency of occurrence (%) of food items in 2,181 lobster stomachs from Kouchibouquac Bay,1965 and 1967. Table condensed from Scarrat (1980).

Stomach content	Range of percentage frequency (%)
Detritus	6.6-92.2
Sand/pebbles	0.8-10.0
Algae	0.2-3.7
Vascular plants	3.8-29.8
Foraminifera	0.2-4.2
Porifera	0.7-8.0
Hydroida	0.5-4.1
Turbellaria	0.5
Bryozoa	0.2
Polychaeta	4.7-27.7
Crustacea	
Copepoda	0.2-4.4
Amphipoda	0.5-8.7
Isopoda	0.5
Cirripeda	0.5-3.0
Cancer irroratus	6.1-41.9
Homarus americanus shell	1.4-12.9
Mysidacea	0.2-11.7
Hyppolitidae	1.7
Mollusca shell fragments	9.6-31.0
Chiton	0.5-5.1
Gastropoda	0.7-3.0
Pelycypoda	0.7-10.0
Mytillidae	10.7-58.1
Echinodermata	
Holothuria	0.5-0.7
Asteroidea	1.3-60.5
Ophiuroidea	1.5-4.8
Echinoidea	14.4-36.8
Tunicata	3.4-38.9
Fish	0.5-5.8

Table 42: Percent frequency of occurrence (%) of food items in stomachs of 288 lobsters from Bonavista Bay, Newfoundland, 1968-1970. Table modified from Ennis (1973).

Stomach content	Frequency of occurrence (%)
Crabs (toad, rock, hermit)	81.3
Unidentified crustaceans	2.4
Scallop, clam, chiton, limpet	22.6
Mussel	28.1
Unidentified shell fragments	17.0
Periwinkle operculae	18.8
Sea urchin	37.2
Sea stars (*Asterias, Leptasterias, Solaster, Ophiophalis)*	24.0
Polychaeta	25.3
Other invertebrates (tunicates, sea anenomes, jellyfish, sponges)	15.6
Fish	10.4
Seaweeds	13.5
Unidentified	45.1
Sand grains	28.5
Rubber, metal, rope fragments	3.1

Table 43: Percentage frequency of occurrence (%) of 1,032 lobster stomachs sampled from Lobster Bay, southwestern Nova Scotia, 1979. Macroalgal site was sampled in August, and barrens in September, 1979, July-August, 1981, and February-March 1982. Values for barrens are the range of reported values for these sampling periods. Table adapted from Elner and Campbell (1987).

Prey taxa	Macroalgal site	Urchin barrens
Animals	100	99-100
Protozoans.Foraminifera	1	5-45
Poriferans	1	0-1
Cnidarians	11	15-22
Bryozoans	1	0-1
Molluscs	94	83-90
Chitons	9	9-34
Tonicella marmorea		2-9
Gastropods	78	4-44
Acmae testudinalis	2	0-2
Lacuna vincta	26	0-6
Skeneopsis striatum	2	0-1
Crucibulum striatum	1	
Crepidula sp.	2	
Lunatia sp.	2	
Mitrella sp.	5	
Bivalves	63	71-87
Mussels (*Mytilus edulis, Modiolus modiolus*)	49	62-85
Cerastoderma pinnulatum	10	0-2
Anomia sp.	4	0-4
Hiatella sp.		0-4
Mya sp.		0-1
Musculus sp.	6	0-2
Polychatetes	54	36-50
Nereis sp.	37	21-37
Polynoids	23	8-24
Spirobis sp.	2	
Cistena sp.	3	0-2
Crustaceans	86	31-79
Barnacles	3	0-2
Isopods	11	0-1
Idotea sp.	3	
Amphipods	23	0.3-3
Corophium sp.	1	0-1
Ampithoe rubricata	10	
Decapods	76	28-74
Homarus americanus	16	2-19
Pagurus sp.	26	0-11
Cancer sp.	30	1-37
Hyas sp.		2-4
Carcinus maenas	2	
Caridion sp.	1	0-1

Table 43 (Con't):

Prey taxa	Macroalgal site	Urchin barrens
Echinoderms	27	29-82
Holothurians	4	0-7
Psolus sp.		0-1
Cucumaria sp.	1	
Strongylocentrotus drobachiensis	1	13-63
Seastars	22	4-21
Ophiuroids	3	6-24
Ophiopholis aculeata		0-9
Amphiopholis squamata	1	
Ascidians	28	0.5-12
Fish	21	0.5-9
Other animals[1]	5	0-3
Plants	83	37-49
Algae	77	37-44
Brown algae	36	5-9
Green algae	14	1-4
Red algae	23	21-33
Tufted red algae[2]		14-29
Corallina officinalis	36	2-15
Zostera marina	2	0-1
Unidentified plant tissue	75	69-100
Gravel	37	3-38
Foreign material[3]	2	0-7
Sample size (n)	115	917

[1] = eggs, nematodes, nemertines, turbellarians
[2] = Family: Ceramiacea
[3] = Plastic, rubber, wood

Table 44: Previous research on sea urchin predation by lobster. Table from Miller (1985).

Experiment type	Prey	Results	Source
Laboratory	Sea urchins only	Killed 1.2% lobster body weight/day	Himmelman and Steele, 1971
Field (Newfoundland)		Urchins comprised 7.1% of lobster stomach volume	Ennis, 1973
Field (St. Margarets Bay)	Urchins and green crabs	Killed 0.4% lobster body weight/day	Breen, 1974
Field (St. Margarets Bay)	Sea urchins only	Killed 2-11% lobster body weight/day	Breen, 1974
Laboratory	Urchins and rock crabs	Killed 0.5% lobster body weight/day	Evans and Mann, 1977
Field (southern Gulf of St. Lawrence)		Urchins comprised 7.2% of lobster stomach volume	Scarrat, 1980
Field (southern Gulf of St. Lawrence)		Urchins comprised 19% of lobster stomach volume	Scarrat, 1980
Laboratory	Sea urchins only	Killed 4.1% lobster body weight/day	Elner, 1980
Laboratory	Urchins and mussels	Killed 0.3% lobster body weight/day	Elner, 1980
Field (Newfoundland)		Urchins comprised 6.6% of lobster stomach volume	Carter and Steele 1982a
Laboratory	Four prey species offered simultaneously	Killed maximum of 4.0% lobster body weight/day	Carter and Steele 1982b

Summary of Benthic Invertebrates Feeding and Diets

The sea star species with available information show different feeding/diet preferences. *Asteria vulgaris* eats a relatively restricted diet of molluscs and echinoderms, appearing to feed quite heavily on *Mytilus edulis*, *Hiatella arctica*, *Chlamys islandica*, *Buccinum undatum* and *Ophiopholis aculeata*. *Crassoster papposus* has a wider range of prey selection including molluscs, echinoderms, cnidarians and urochordates. Principle prey species for *C. papposus* are sea urchins, and the sea stars *Leptasterias polaris*, *Ophiopholis aculeata*, and *Asterias vugaris*. *Solaster endeca* has the most restricted diet, feeding only on echinoderms and appearing to concentrate on *Psolus fabrici* and *Echinarachinus parma*. *Leptastarias polaris* feeds on a very broad selection of prey items and does not appear to concentrate heavily on any species, though the mollucs *Mytilus edulis*, *Hiatella arctica*, *Mya truncata*, and *Buccinum undatum* are the most commonly encountered stomach contents in *L. polaris*.

The dominant food of the green sea urchin is brown algae, though it does feed extensively on other algal species as well. Barnacles, mussels and small gastropods are also consumed by the sea urchin.

There are very limited data on food habits of whelks in Atlantic Canada. Though they are known to feed on animals such as clams and crabs, it is suggested that their diet is largely composed of soft bodied organisms.

A large component of the diet of the green [shore] crab is composed of bivalve and gastropod molluscs, algae, and marine plants. *Mytilus edulis* and *Mya arenia* contribute significantly to the stomach contents while other crabs and crustaceans formed only a small proportion of material in the stomachs of 4,741 green crabs. The snow crab preys to a large degree on polychaetes other crabs, crustaceans, and molluscs. As a generalization, based on the 1,255 samples reported in the papers summarized here, the frequency of occurrence appears to be polychaetes>crustaceans>molluscs. Plant material and cannibalism also form componenets of the diet of this crab. Results from 569 rock crab stomachs indicate that these crabs appear to prey most heavily on polychaetes, the mussel *Modiolus modiolus*, other crustaceans, and the green sea urchin. They appear to have a clear preference of mussels over urchins, and there is evidence of rock crab predation on lobsters.

Larval lobster feed on zooplankton, particularly *Podon*, *Temora*, *Acartia*, *Pseudocalamus*, and *Centropages*. Immature lobsters (n=103) have a diet similar to adults but differing in proportions of components. These immature lobsters feed on a large selection of items with few obvious preferences. Sea urchin, mussels, rock crab larvae, and various polychaetes turn up most commonly in their stomachs, but there is a large variety of other food which these immature animals eat. The adult lobster, generalized from the results of 3,676 stomachs, consume a very large array of foods with the more commonly consumed species appearing to be pelycypod molluscs (*Modiolus*

modiolus and *Mytilus edulis*), crustaceans (particularly rock crabs), polychaetes, sea stars, urchins, algae and vascular plants.

This review of invertebrate feeding and diets is neither exhaustive nor comprehensive. It is instructive, however, as a rough guide of what diet research has been done, and, conversely, what is required. Though the feeding of the lobster and crab species are quite well studied and known, they form a relatively small component of the benthic community. For example, Himmelman and Hamel (1993) report that earlier studies have shown the whelk *Buccinum undatum* to be the most abundant carnivore present (over 4 times more abundant than the next most common carnivore, *Leptasterias polaris*, and 15 time more abundant than other sea stars, crabs and fishes). Historically and at present the commercially important species, or those that interfere with these species (e.g., urchins and sea stars), are those which are researched and documented. However, in order to comprehend and begin to understand the trophic dynamics of the benthic communities, and their interactions with the overlying communities in the water column, more emphasis on the myriad of as yet unstudied, commercially neutral invertebrate and vertebrate species is necessary.

3.b. Feeding of Benthic Fish

PLEURONECTIDAE · RIGHT-EYED FLOUNDERS

The Family Pleuronectidae, or right-eyed flounders, are generally bottom feeders which prey heavily upon benthic and infaunal organisms, chiefly crustaceans, polychaetes and echinoderms (Methven, 1999), although there is variation among species. American plaice is estimated to provide the largest biomass component of fish within St. Georges Bay. Winter flounder contributes about half this biomass and witch flounder is present in volumes on par with a number of other fish species (Appendix 3). Yellowtail and smooth flounder are also identified as being present in St. Georges Bay (Kenchington, 1980). As each of these feed within the same habitat, one would expect modes of resource partitioning that reduce interspecific competition to be found within the group.

American plaice, yellowtail and winter flounder are species that are found, in order of listing, in progressively shallower waters (Scott and Scott, 1988). This mode of distribution may occur within St. Georges Bay, although this has not been documented. Seasonal migration patterns of these species in the southeastern Gulf have been shown to follow a predictable succession. With decreasing autumn temperatures, the deeper-water species leave the shallows of St. Georges Bay first, and the winter flounder leave last (Clay, 1991). Thus the variability in the species' ability to withstand broad ranges in temperature allows for differential use of the habitat's resources.

American plaice have large gapes relative to other flounders (Scott and Scott, 1988) and are therefore less restricted in prey selection by prey size. Bowman et al. (1984) describe the plaice mouth as being best adapted for eating larger prey on the bottom. Hacunda (1981) observed prey size distribution between winter and yellowtail flounder to vary, respectively averaging 6.8 ± 3.0 and 10.8 ± 4.9 mm with a bimodal distribution.

Armstrong (1997) observed spatial partitioning within estuaries and open bay habitat between smooth and winter flounder; the former remaining in the upper estuary while the latter was distributed more within the open bay.

Table 45 presents percent frequency of diet items of four flounders on the Scotian Shelf (Scott, 1982), illustrating the variation occurring within one geographical location. The data represents fish as an important prey item for each pleuronectid, based on the percent of stomachs in which they occur. However, there is variation in the degree to which fish is consumed by each species, ranging from 56.7 % for the yellow flounder, to 86.3 % frequency for winter flounder. Crustaceans, polychaetes and bivalves are all prominent diet components for winter, yellowtail, and witch flounder; in contrast, brittlestars are more prominent in American plaice diet.

Table 45: Percent occurrence of prey groups of flatfish on the Scotian Shelf, Scott (1982).

	Winter flounder	Yellowtail flounder	American plaice	Witch flounder
Fish	86.3	56.9	68.4	72.5
Crustaceans	73.2	80.9	38.7	49.9
Polychaetes	74.3	57.3	15.7	85.9
Lamellibranchs	41.0	39.0	13.6	32.2
Tube worms	4.9	9.0	7.2	6.2
Sand dollars	10.9	19.3	3.9	-
Sea urchins	0.5	12.1	10.7	-
Brittlestars	0.5	11.3	45.4	2.6
Gastropods	3.8	17.7	8.8	10.0
Pandalid shrimp	0.0	0.4	8.6	-
Crabs	1.1	0.4	0.6	-
Hermit crabs	1.6	-	3.1	-
Isopods	2.7	0.2	4.0	0.4
Starfish	-	-	0.9	-
Miscellaneous	-	-	2.2	-
Number of stomachs	183	384	668	469

American Plaice *Hippoglossoides platessoides*

American plaice necessarily have a significant role in the ecosystem of St. Georges Bay, based solely on relative biomass estimates. Prey includes varying proportions of all or most of the following groups: echinoderms, polychaetes, crustaceans, molluscs and fish, depending on location (Methven, 1999).

Studies of diets specific to St. Georges Bay have not been found, although foundation work has been carried out for the southern Gulf of St. Lawrence. Table 46 represents estimates drawn from graphed data (Appendix 5) published by Scott (1973a) as well as studies from the Magdalen Shallows and Scotian Shelf, expressed in percent occurrence of prey items. Each study identified polychaetes, echinoderms (brittlestars) and fish as the major prey items. The results were comparable among locations except for the more frequent occurrence of crustaceans in diets in the southern Gulf relative to the two other sites, and the relatively low occurrence of polychaetes and fish in the Magdalen Shallows American plaice diet. Scott (1973a) observed variation within the Southern Gulf, which reflected local differences in prey availability.

Table 47 presents percent weight of prey species from various offshore locations. Variation in diet by location in this data set appears much greater than that which is reported as percent frequency, presented in Table 46. Sampling south of the Grand Banks revealed very low consumption of fish, whereas it is a large diet component in Newfoundland waters (Pitt, 1973; Methven, 1999). Langton and Bowman (1981), and Bowman et al. (1976) report diets largely composed of brittlestars (*Ophiura sarsi*,

Table 46: Percent occurrence of prey groups in stomachs of American plaice for southern Gulf of St. Lawrence (area 4T), Magdalen Shallows and Scotian Shelf.

	Southern Gulf [1] 1971,1972 Scott (1973a)	Magdalen Shallows [2] 1957 Powles (1965)	Scotian Shelf Scott (1981)
Annelids	18	7	15.7
Crustaceans	76	32	38.7
Pelecypods	13	20	13.6
Gastropods	0	0	8.8
Echinoderms	·	49	·
Brittlestars	66	·	45.4
Sand dollars	3	·	3.9
Urchins	0	·	10.7
Fish	59	2	68.4
Number of stomachs	157	561	668

1 estimated from graphed data, corrected for numbers within size classes
2 estimated from graphed data

Table 47: Stomach contents of American plaice from Northwest Atlantic sites.

	New England 1969-1972 Langton and Bowman (1981)	Georges Bank 1969-1972 Langton and Bowman (1981)	Gulf of Maine 1969-1972 Langton and Bowman (1981)	W.Nova Scotia 1969-1972 Langton and Bowman (1981)	Southern Grand Bank 1964-1971 Pitt (1973)
Cnidaria	-	**<0.1**	**0.5**	**0.3**	**1**
Annelids	**18.2**	**0.4**	**9.5**	**3.9**	-
Arthropods	**57.6**	**7**	**12.5**	**30.2**	**8**
Molluscs	**10.6**	**0.3**	**22.6**	**1.3**	**1**
Gastropods	-	0.1	<0.1	1.0	-
Bivalves	10.6	<0.1	22.3	0.2	1
Echinoderm	**3.8**	**90.7**	**45.9**	**55.3**	**7**
Urchins	-	72.2	7.1	43.4	3
Brittlestars	3.8	18.5	38.8	11.9	4
Fish	-	**0.3**	**2.2**	**0.6**	**83**
Other	2.8	0.1	1.7	0.2	.
Remains	7	1.2	4.2	3.1	.
Stomachs	31	287	562	306	.
% Empty	58.1	48.4	35.2	40.9	.

O. robusta), sand dollars (*Echinarachnius parma),* and urchins (*Strongylocentrus droebachiensis*) in the Northwest Atlantic.

Variation in diet among sites south of Newfoundland is notable for New England, as American plaice feed more heavily on arthropods (57.6 %) and annelids (18.2 %) rather than echinoderms, which is the prey consumed in largest proportions in the three other sites.

Powles (1965) observed change in diet with size of American plaice in the Magdalen Shallows. Crustaceans (mysids, amphipods, krill, decapods and cumaceans) were dominant in the diet of fish less than 15.0 cm long, but contributed only 10 - 20 % of the diet of fish greater than 40 cm. This was also found throughout the southern Gulf. As well, pandalid shrimp were of importance only to fish within the 15 – 20 cm range (Scott, 1973a). Urchins, brittlestars and tubeworms were consumed in greater proportions by larger American plaice. Increased reliance on echinoderms is a transition to a relatively nutrient-poor diet, but Scott (1973a) suggests that the size and abundance of prey compensate for this. In the Northwest Atlantic, Bowman et al. (1987) reported that polychaetes and amphipods comprised the largest proportion of the diet of the 6 - 10 cm size-class.

Data collected by Scott (1973a) presented in Appendix 5 illustrates a heavier reliance on crustaceans (amphipods and mysids) and polychaetes among fish up to 40 cm in length, an increase of predation on fish among smaller predators, and an increased consumption of echinoderms with size. Variation in diets among regions within the Gulf of St. Lawrence appears from this data to be restricted to echinoderm consumption.

Seasonal variation in feeding intensity was observed as extreme reduction of feeding from January to March (Powles, 1965), and increased feeding intensity in June and July.

Winter Flounder · *Pseudopeuronectes americanus*

The winter flounder is noted for its persistence in colder shallow waters late into the winter, attributed to its production of anti-freeze polypeptides. Although the population leaves the St. Georges Bay ecosystem as late as January, it also returns later than other species, in June (Clay, 1991). Thus, differences in migrational timing may result in a lower relative impact on St. Georges Bay biomass consumption, as a relatively larger portion of their time spent in the Bay is during their period of low feeding activity (Scott and Scott, 1988).

Winter flounder feed during the day, predominantly on polychaetes, and are described as generalists (McEachran et al., 1976) which feed on any prey of suitable size (restricted by small gape size) encountered while foraging. Langton and Bowman (1981) state that diet reflects that they are bottom feeders, and feed largely on polychaetes, bivalves and crustaceans. Wells et al. (1973) report that the large intertidal areas of the

Bay of Fundy are major feeding grounds for the winter flounder. The inshore feeding habit of coastal winter flounder is not reflected in Northwest Atlantic data, but is represented by the presence of plant material in Kennedy and Steele (1971), presented in Table 48.

Diet analysis from the southern Gulf of St. Lawrence (Scott, 1976) presented fish remains, polychaetes, crustaceans (amphipods) and bivalves as important prey by percent incidence (Table 48). This is reflective of a generalist feeder, which does not specialize on specific prey types. Little variation in diet with size was reported. Data from the Avalon Peninsula, Newfoundland (Kennedy and Steele, 1971) is also presented as percent incidence and percent weight for comparison. This data represents considerable consumption of gastropods, not observed in the Gulf, apparently compensating for a reduced consumption of fish.

Table 48: Percent occurrence of prey groups in winter flounder stomachs from the southern Gulf of St. Lawrence, by size class, and Newfoundland inshore.

	Southern Gulf, Scott (1976) % occurrence				Avalon Peninsula 1962,1963 Kennedy and Steele (1971)	
	< 25 cm	25-29cm	30-34cm	>34cm	% occurrence	% weight
Cnidarians	.	.	.	.	**3.5**	**1.8**
Polychaetes	**87.5**	**100**	**95.7**	**100**	**62.5**	**17.2**
Bivalves	**93.75**	**75**	**31.9**	**10**	**69.6**	**5.8**
Gastropods	-	-	-	-	**30.7**	**0.8**
Crustaceans	**100**	**100**	**91.5**	**100**	**48.4**	**1.2**
Isopods	6.25	2.5	-	-	.	.
Crabs	-	-	-	-	0.3	0.0
Echinoderms	**25.5**	**25**	**12.8**	-	**4.3**	**0.5**
Fish	**87.5**	**82.0**	**78.7**	**100**	**4.3**	**15.3**
Fish eggs	.	.	.	.	12.5	7.2
Plant material	.	.	.	.	**24.0**	**12.6**
Debris	.	.	.	.	79.5	14.4

Table 49 presents percent weight of prey groups for various Atlantic regions. Fish consumption is a notably smaller proportion by weight in these areas as reported by Pitt (1971). Algae is significant in coastal diets, and diversity of diet generally increases inshore (Methven, 1999).

Langton and Bowman (1981) report considerable variation among North Atlantic sites. A variety of annelids, and molluscs, particularly bivalves are significant to all locations; crustaceans, mostly amphipods and decapods contributed large diet components to southern New England and western Nova Scotian flounder. Hacunda (1981) observed greater consumption of crustaceans (32.5 %) in the Gulf of Maine.

Table 49: Stomach contents of winter flounder for various Atlantic sites, percent weight.

	S. New England, 1969-1972 Langton and Bowman (1981)	Georges Bank 1969-1972 Langton and Bowman (1981)	Gulf of Maine 1969-1972 Langton and Bowman (1981)	Western Nova Scotia 1969-1972 Langton and Bowman (1981)	Gulf of Maine 1978-1979 Hacunda (1981)
Cnidarians	**10.1**	**30.4**	**0.4**	**17.4**	.
Nemertea	.	.	.	.	**0.16**
Polychaetes	**38.6**	**15.1**	**60.5**	**55.8**	**18.26**
Molluscs	**12.5**	**20.4**	**4.8**	**4.3**	**6.09**
Bivalves	12.5	20.3	4.8	2.8	5.13
Gastropods	< 0.1	0.1	-	1.1	0.96
Crustaceans	**13**	**3.9**	**1.9**	**9**	**32.5**
Echinoderms	**7.4**	**0.5**	**0.1**	**0.7**	**0.50**
Pisces	**0.3**	**0.1**	**0.5**	**0.2**	-
Other	6.1	2.6	4	7.7	-
Remains	8.9	20.4	27.6	3.7	15.03
Sand, rock	3.1	6.6	0.2	1.2	-
No. stomachs	154	321	120	128	201
% empty	64.3	35.5	37.5	10.9	28.4

Feeding intensity was greater in spring and summer and tapered off in fall in Newfoundland. Patterns in seasonal variation in food items were not strong, although polychaete consumption was higher and gastropod and copepod consumption was lower in March than in the rest of the summer and probably reflected prey availability (Kennedy and Steele, 1971).

Witch Flounder · *Glyptocephalus cynoglossus*

Witch flounder diet is composed of polychaetes, amphipods, small fish, bivalves and snails, all small in size due to the limitation of predator mouth size (Scott and Scott, 1988). Although its distribution is known to be widespread in the Gulf of St. Lawrence, it is rarely abundant (Kenchington, 1980).

Diet studies for the Southern Gulf were not found, however, Langton and Bowman (1981) report diet data for several sites from the Atlantic Ocean, which is presented in Table 50. Polychaetes dominate the diet of witch flounder at all sites except southern New England, where squid become significant. The importance of polychaetes is typical of reported witch flounder diets. Crustaceans are also a significant diet component; Bowman and Michaels (1984) report similar patterns for these same sites in their investigations.

Rae (1969) reports similar findings in the eastern Atlantic, observing a slight shift in consumption from amphipods and cumaceans towards polychaetes with increased size. Comparisons of studies indicate only small influences in diet due to environment

Table 50: Percent weight of prey items for witch flounder from four Atlantic areas collected from 1969 to 1972, Langton and Bowman (1981).

	S. New England	Georges Bank	Gulf of Maine	Western Nova Scotia
Cnidaria	**0.5**	**-**	**1.4**	**3.1**
Annelids	**42.0**	**87.8**	**81.8**	**60.0**
Arthropods	**12.1**	**6.2**	**3.2**	**11.4**
Molluscs	**40.4**	**0.2**	**0.4**	**0.8**
Gastropods	-	-	<0.1	0.1
Bivalves	0.1	0.2	0.4	0.6
Cephalopods	40.3	-	< 0.1	< 0.1
Echinoderms	**-**	**0.2**	**4.9**	**16.3**
Sea cucumbers	-	0.2	4.5	16.3
Sea urchins	-	-	-	-
Brittlestars	-	-	0.4	< 0.1
Fish	**0.4**	**-**	**1.2**	**0.1**
Others	**<0.1**	**0.3**	**1.3**	**2.5**
Remains	4.6	5.2	5.4	5.5
No. stomachs	94	98	597	338
% empty	37.2	6.1	7.5	6.2

and prey availability (Langton and Bowman, 1981). Bowman and Michaels (1984) observed consumption of krill, *M. norvegica* to comprise 69.8 % of < 20 cm flounder diets and 34.9 % of 26-30 cm long flounder diet. As the percent of crustaceans in diet declines with size, the portion of echinoderms, chiefly sea cucumbers, increases.

Bowman et al. (1987) report that juveniles up to 5 cm in length prey strictly on crustaceans, particularly gammarid shrimp (87.3 %) and also mysids, chiefly *N. americana* (12.7 %). Larger juveniles, of lengths 6 – 10 cm feed on 38.2 % polychaetes, *Ampharetidae* and *Sabellidae* and 34.8 % of the diet is composed of the decapod crangon.

Yellowtail Flounder · *Limanda ferruginea*

Yellowtail flounder distribution has been reported to be throughout St. Georges Bay, although concentrated more towards the mouth of the bay. They enter the bay in the spring, and numbers are found to decline in August and September (Kenchington, 1980). Feeding by the yellowtail flounder is restricted by small mouth size (Scott and Scott, 1988). Crustaceans and polychaetes found on the sediment surface constitute large components of the yellowtail flounder diet (Methven, 1999). Data presented in Table 51 illustrates this pattern with data reported from various sites.

Langton and Bowman (1981) report that annelids and arthropods contribute similar diet proportions at all sites, except western Nova Scotia, where one genus, *Eunice*, contributed 66.8 % of the diet by weight. Among crustaceans, amphipods were

Table 51: Diet of yellowtail flounder in Atlantic sites reported by various authors.

	Gulf of Maine 1978-1979 Hacunda (1981)	Grand Banks 1968-1973 Pitt (1976)	S. New England, 1969-1972 Langton and Bowman (1981)	Georges Bank 1969-1972 Langton and Bowman (1981)	Gulf of Maine 1969-1972 Langton and Bowman (1981)	Western Nova Scotia 1969-1972 Langton and Bowman (1981)
Porifera	.	**0.5**	.	.	.	.
Cnidaria	.	**1.6**	**0.2**	**10.3**	**1.9**	**6.3**
Nemertea	**3.5**	.	.	.	.	.
Annelids	**10.15**	**38.0**	**34.5**	**47.2**	**27.7**	**81.1**
Molluscs	**5.19**	**2.8**	**1.6**	**1.5**	**0.2**	-
Bivalves	**5.19**	**2.8**	**1.2**	**1.2**	**0.2**	-
Gastropods	-	< 0.1	0.2	0.2	-	-
Arthropods	**48.5**	**35.1**	**46.3**	**32.3**	**27.7**	**7.7**
Cumaceans	0.45	0.1	0.6	0.1	-	-
Amphipods	33.58	29.3	41.1	28	26.3	7.4
Krill	.	4.0	<0.1	-	-	-
Mysids	12.51	< 0.1	< 0.1	< 0.1	-	-
Decapoda	1.59	< 0.1	3.5	3.5	1.1	0.2
Isopoda	0.37	0.8	.	.	.	.
Echinoderms	**0.05**	**6.9**	**2.1**	**2.3**	**21.0**	**0.2**
Brittlestars	.	4.5	< 0.1	< 0.1	-	0.1
Sea cucumbers	.	0.4	0.2	0.3	20.9	0.1
Sea urchins	.	2.1	1.9	2.0	0.1	< 0.1
Others	.	2.5	.	.	.	.
Fish	**0.05**	**7.5**	**0.3**	**0.1**	-	**0.4**
Unidentified	**16.38**	**<0.1**	**8.3**	**2.1**	**4.9**	**3.3**
Detritus	16.2	3.6	.	.	.	.
No. stomachs	60	11.34	1,415	652	44	70
% empty	23.3	32.8	21.4	25.7	29.6	40.0

the largest diet component at all locations (Bowman and Michaels, 1984; Efanov and Vinogradov, 1973; Collie, 1986).

Pitt (1976) found that fish was a significant component of the diet on the Grand Banks, particularly capelin and sand lance. He also reports that there was little variation in diet with size of predator.

Juvenile yellowtails from 1 to 5 cm in length, consume crustaceans solely, chiefly decapods, *Crangon septemspinosa*. Beyond this size class, crustaceans comprise about one half of the diet weight and polychaetes and fish make up most of the remainder (Bowman et al., 1987).

Smooth Flounder · *Liopsetta putnami*

The smooth flounder is a shallow-water fish, common to the mud or silt bottoms of estuaries, where it feeds mainly on marine worms, amphipods, small molluscs, shrimp and crabs (Scott and Scott, 1988). Few reports on diet have been produced. Only one smooth flounder was found during extensive sampling of St. Georges Bay. This fact, in addition to the lack of recognition of the fish by local fishers, suggests that there are few, but perhaps they are more abundant in the estuaries of the bay (Kenchington, 1980).

A study of the Mirimachi estuary smooth flounder population (Hanson and Courtenay, 1997) demonstrated that they occur largely upstream in spring and summer during their peak of feeding activity and then move to the lower estuary or to the ocean in the fall and winter when feeding is very limited. Thus, their interaction within the marine ecosystem is minimal.

Hanson and Courtenay (1997) found that bivalves represented most of their prey, varying from 14.7 % to 94.6 % over varying feeding periods and size classes; and shrimp contributed a significant amount to the diet in the late fall. Other prey present in small amounts were sand shrimp, crabs, and polychaetes. With the exception of the smallest size group, feeding peaked in May and June and gradually decreased to nil in January. Clam consumption peaked in May, and decreased through the summer months, and increased again in the fall. The volume of unidentified prey peaked during this time, so perhaps the decrease in consumption is an artifact associated with different digestion rates in the summer. The largest size class showed increased consumption of *Calanus* during the summer.

Smaller smooth flounder (5 - 9.9 cm) fed most intensively in May, gradually decreasing feeding as did the larger size classes, until the winter.

BOTHIDAE

Windowpane · *Scophthalmus aquosus*

The windowpane is the only representative of the left-eye flounders reported in St. Georges Bay. It is a carnivorous, shallow-water resident, and is known to feed on sand shrimp, and small tomcod, smelt, hake, pollock, striped bass and herring in the Bay of Fundy (Scott and Scott, 1988).

Bowman et al. (1976) found marked differences in Northwest Atlantic sites reported in 1976; although crustaceans were significant prey groups at both sites, they comprised 99 % of the diet in southern New England (Table 52). The corresponding value for Georges Bank was 28.6 %, while echinoderms constituted 50.3 % of the diet there.

Langton and Bowman (1981) sampled these same sites, and found in both study areas that pelagic crustaceans were the largest prey group. Wider variation in crustaceans were consumed, as well as fish, contributing 3.1 % and 13.1 % to the diet of New England and Georges Bank windowpane diets, respectively. Sand lance, silversides, longhorn sculpin and windowpane contributed to the Georges Bank fish prey. The diet of the young were found to be largely mysids.

Table 52: Percent weight of prey items found in windowpanes at two Atlantic sites.

	S. New England Bowman et al. (1976)	Georges Bank Bowman et al. (1976)	S. New England Langton and Bowman, (1981)	Georges Bank Langton and Bowman, (1981)
Arthropods	**99.0**	**28.6**	**92.0**	**77.0**
Amphipods	-	-	3	0.8
Caridean shrimp	13.7	26.7	3.3	45.9
Pandalid shrimp	.	.	33.5	6.7
Brachyuran crabs	-	-	.	.
Mysids	80.5	-	50.8	20.4
Krill	.	.	-	0.4
Unknown	4.8	1.9	.	.
Other	.	.	1.4	2.3
Molluscs	.	.	**1.7**	-
Sea urchins	-	**50.3**	-	**3.3**
Fish	.	.	**3.1**	**13.1**
Animal remains	0.3	21.1	1.9	4.9
No. stomachs	45	30	318	228
% empty	22.2	60	43.1	39.5

ZOARCIDAE

Ocean pout *Macrozoarces americanus*

Ocean pout are non-visual bottom feeders. They are believed to gather material from the substrate and eject debris, thus they ingest infaunal and epifaunal material which consists mainly of urchins, various molluscs and crustaceans (Methven, 1999).

The ocean pout demonstrates great adaptability in diet, illustrated by the variability in importance among and within crustacean, echinoderm, and mollusc prey groups. Table 53 presents results from a number of Northwest Atlantic sites.

Keats et al. (1987) collected ocean pout from a rocky subtidal area with a large population of urchins. A large proportion (62 %) of the observed diet of the eastern Newfoundland ocean pout is the green sea urchin, *Strongylocentrotus droebachiensis*,

Table 53: Stomach contents of ocean pout collected from Northwest Atlantic sites.

	Georges Bank Buzulut-skaya(1983)	Nantucket shoals Buzulut-skaya(1983)	Gulf of Maine Hacunda (1981)	Eastern Nfld Keats et al. (1987)	S. New England 1969-1972 Bowman et al. (1976)	Gulf of Maine 1969-1972 Bowman et al. (1976)
Cnidaria	.	.	.	.	-	**1.0**
Annelids	.	.	**1.41**	**< 0.01**	**10.3**	**0.5**
Crustaceans	**38.6**	**83.8**	**13.65**	**0.15**	**25.8**	**3.8**
Mysids	.	.	0.14	.	.	.
Cumaceans	.	.	2.12	.	0.1	-
Amphipods	36.3	7.8	10.29	.	13.4	0.3
Decapods	2.3	76.0	1.08	.	7.5	2.5
Molluscs	**0.5**	**8.5**	**9.78**	.	**0.5**	**5.7**
Bivalves	0.5	8.5	9.57	0.24	0.4	5.6
Gastropods	.	.	.21	-	.	-
Unidentified	-	-	.	.	0.1	0.1
Echinoderm	**43.7**	**1.2**	**20.63**	**61.9**	**59.2**	**75.7**
Brittlestars	.	.	0.82	.	-	8.9
Sea urchins	.	.	19.81	61.9	59.2	66.8
Tunicates	.	.	.	.	-	**0.6**
Nematodes	**11.0**	**24.0**	.	.	.	.
Fish eggs	.	.	.	**8.05**	-	**6.2**
Fish	.	.	.	**19.88**	**0.1**	-
Detritus	.	.	**37.55**	**0.84**	.	.
Unidentified	17.2	6.5	6.99	0.89	3.6	5.9
No. stomachs	43	46	46	151	129	109
% empty	21.0	15.0	10.9	35.1	16.3	31.2

mostly under 5 mm in size. Keats et al. (1987) suggest that because the pout consumes a narrow segment of the population intensively, it has potential to influence the urchin's population.

Hacunda (1981) found that urchins contributed the largest proportion by weight to diets of the ocean pout along the coast of Maine. Crustaceans, particularly amphipods, were also consumed in significant amounts; Busulutskaya (1983) found this same pattern on Georges bank, however on the Nantucket shoals, there was an heavy reliance (86%) on crustaceans, chiefly the crab, *Cancer borealis*.

Busulutskaya (1983) found that small ocean pout feed mainly on crustaceans; with increased size, consumption of gammarids gave way to *Cancer* sp.

Vahl's eelpout · *Lycodes vahlii*

Vahl's eelpout, or the checker eelpout is a subarctic fish which feeds on polychaetes, small crustaceans and molluscs (Scott and Scott, 1988). This species is expected to occur in the bay, but was not found during an extensive survey carried out in 1978 (Kenchington, 1980).

RAJIDAE . SKATES

The family Rajidae are bottom feeding carnivores which prey upon crustaceans, polychaetes, bivalves, and small fish. Three species are known to be represented in St. Georges Bay, the thorny skate (*Raja radiata*), the little skate (*Raja ericacea*), and the winter skate (*Raja ocellata*). The barndoor skate, *Raja laevis*, has historically been common to this area and is therefore thought to reside in the Bay, although in small numbers (Kenchington, 1980).

Thorny skate · *Raja radiata*

Diet of the thorny skate includes polychaetes, amphipods, decapods and fish, (Scott and Scott, 1988). Templeman (1982) found fish to comprise 74 % of the Northwest Atlantic thorny skate diet and invertebrates to contribute 24 % by volume. Redfish, haddock, sand lance, and fish offal of cod and haddock represented fish prey (Table 54). Crabs, cephalopods and polychaetes comprised the invertebrate prey. This data is a compilation of data from West Greenland to Georges Bank collected over the period of 1947 to 1967, thus it does not represent geographical variation. The author notes that diet variation would occur as a result of variation in abundance. Less than 1 % of these skate stomachs were collected from the Gulf of St. Lawrence.

Table 54: Stomach contents of 446 thorny skates collected from West Greenland to Georges Bank, 1947-1967 (Templeman, 1982).

	Percent volume
Invertebrates	**25**
Crabs	14
Cephalopods	5
Polychaetes	4
Fish	**74**
Redfish	18
Haddock	14
Sand lance	12
Offal	17

Smaller skates were found to consume more crabs, cephalopods, polychaetes and amphipods than skates larger than 61 cm. Larger skates relied more on fish, which comprised 78 % of the diet by weight (compared to 35 % in smaller skates) and consumed it in wider variety (Templeman, 1982). Tyler (1972) also reported smaller skates eating smaller prey than the polychaete prey of adults.

Variation in fish species consumed was observed among fish collected at differing depths, thus suggesting a representation of varying prey distribution. Skates collected at shallower depths (to 200 m) contained more haddock, which was replaced by redfish in the diets of skates collected from greater depths.

Little Skate · *Raja erinacea*

The little skate is associated with shallow waters, over substrates of sand or gravel. In the Passamoquaddy Bay in Maine, these fish are known to enter near-shore waters in the fall, and leave in the spring, following cold water temperatures, rather than warm (Tyler, 1972).

Table 55 presents stomach contents of the little skate collected from New England and Georges Bank, in percent weight, during 1973 – 1976. This data, reported by Bowman and Michaels (1984), reports crustaceans as the dominant prey of little skates. There was a shift from consumption of amphipods (*U. irrorata, G. annulatus, L. piguis* and *M. edwardsi*) in young skates (<35 cm), to decapods *(C. borealis, C. irrorratus, C. septemspinosa, P. acadianus* and *D. leptocerrus*) in larger skates. Bowman et al. (198?) report less variety in the prey field of 6 -10 cm size class. Polychaetes, molluscs and small fish (< 20 cm length) were also preyed upon.

Table55: Diet of little skates in New England and Georges Bank, 1973-1976, presented as percent weight of stomach contents, Bowman and Michaels (1984).

	S. New England	Georges Bank
Cnidaria	**1.4**	**0.2**
Nemertea	**0.5**	**1.1**
Polychaetes	**15.5**	**8.7**
Crustaceans	**61.4**	**72.0**
Amphipods	22.9	10.1
Decapods	30.5	56.6
Isopods	2.0	0.9
Other	6.0	4.4
Molluscs	**4.8**	**0.7**
Bivalves	2.9	0.5
Other molluscs	1.9	0.2
Fish	**4.8**	**6.8**
Radiated shanny	-	3.2
Other fish	4.8	3.6
Miscellaneous	**11.6**	**10.5**
Stomachs	486	579
Empty stomachs	35	62

Previous sampling in these two locations found very similar results, but with less emphasis (10 % in both sites) on the diet of crustaceans (Bowman et al., 1976). A greater variety of fish were found as prey in the previous study, composed of pleuronectids, gadids, cottids and fish eggs.

Winter skate · *Raja ocellata*

The winter skate is a benthic predator, with an affinity for colder water, collected from temperature ranges of –1.2 to 4.8°C in the Gulf of St. Lawrence (Scott and Scott, 1988).

Clay (1991) reports that the winter skate moves to depths greater than 40 m as late as December, remaining in cold water longer than most other species of St. Georges Bay. They feed chiefly on amphipods and polychaetes, but fish (sand lance), decapods, isopods and bivalves are also part of the diet (McEachran et al., 1976).

COTTIDAE

Longhorn sculpin · *Myoxocephalus octodecemspinosus*

The longhorn sculpin represents a significant portion of the fish biomass of St. Georges Bay, but there is surprisingly little literature available on this species or other members of the Cottidae family in the region. This sculpin is a year-round resident of coastal waters, preferring colder water and migrating to deep water in the summer at its southern distribution limit. It is a voracious carnivore (Scott and Scott, 1988) feeding on a variety of prey.

Bowman et al. (1976) found that crustaceans constitute most of the sculpin's diet (Table 56). Crabs were the most significant crustacean prey at most sites studied in the Northwest Atlantic, however, krill were also consumed in large proportions in western Nova Scotia. Polychaetes and fish (sand lance, pleuronectids, and sculpin) were small proportions of the sculpin diet.

Bowman and Michaels (1984) examined longhorn sculpin diet on Georges Bank and reported results differing from those of Bowman et al. (1976). Bowman and Michaels (1984) found amphipods, including *U. irrorata*, and *L. pinguis*, and the small decapods, *C. irroratus*, *H. coarctatus*, *Pagurus* sp. and *D. leptocerus* to contribute a large

Table 56: Diet of longhorn sculpin collected at sites in the Northwest Atlantic, 1969 - 1973, percent weight, Bowman et al. (1976).

	S. New England	Georges Bank	Gulf of Maine	W. Nova Scotia
Nemertea	.	**0.1**	**3.0**	-
Annelids	**4.8**	**2.6**	**9.3**	**2.8**
Molluscs	**1.0**	**1.1**	-	-
Bivalves	0.2	0.7	-	-
Gastropods	-	0.2	-	-
Unidentified	0.8	0.2	-	-
Crustaceans	**84.0**	**81.8**	**56.3**	**78.5**
Cumaceans	0.1	-	-	-
Amphipods	9.0	1.2	3.7	0.1
Krill	0.3	0.1	-	19.5
Mysids	-	0.1	-	-
Decapods	**47.3**	**73.2**	**49.9**	**52.7**
Isopods	3.4	0.5	2.7	-
Unidentified	23.9	6.7	-	6.2
Fish	**8.0**	**11.2**	**11.2**	**9.2**
Animal remains	1.9	2.0	20.2	8.0
Sand and rock	0.3	1.0	0	1.5
No. stomachs	453	287	50	80
% empty	26.3	37.3	66	28.8

proportion of the diet. Isopods, mysids and polychaetes were also consumed whereas fish contributed minor proportions. Hacunda (1981) found fish prey to contribute a larger proportion to the Maine sculpin diet (25.19 %), while crustaceans constituted less of the diet (58.42 %) than reported by Bowman and Michaels (1984).

Juvenile longhorn sculpins have been shown to feed largely on small decapods, amphipods, and on isopods in smaller amounts (Bowman et al., 1987).

Sea raven · *Hemitripterus americanus*

The sea raven is a benthic fish, living on rocky or hard bottoms, feeding on invertebrates, herring, sand lance and silver hake (Scott and Scott, 1988).

Bowman et al. (1976) found sea ravens to eat significant amounts of fish (59.6 – 75.8 %) at sites studied in the Northwest Atlantic (Table 57). The fish were largely unidentified, but on the Georges Bank 40.0 % of the prey by weight were sculpin. Molluscs were significant to Georges Bank and Gulf of Maine sea ravens, but absent from the southern New England diet. Crustaceans, instead were a significant prey group in southern New England.

Table 57: Diet of the sea raven, collected during 1969 – 1972, percent weight (Bowman et al., 1976).

	S. New England	Georges Bank	Gulf of Maine
Nemertea	**0.1**	-	**0.6**
Annelids	**0.1**	-	-
Molluscs	-	**22.1**	**37.9**
Cephalopods	-	22.1	37.9
Crustaceans	**32.0**	**2.1**	**1.9**
Decapods	31.7	2.0	1.4
Mysids	-	-	0.5
Unidentified	0.3	0.1	-
Fish	**66.1**	**75.8**	**59.6**
Right-eye flounders	-	0.2	-
Gadids	6.2	18.2	-
Cottids	-	40.2	-
Unidentified fish	59.9	17.2	59.6
Sand and rock	1.7	-	-
No. stomachs	11	66	7
% empty	45.5	43.9	14.3

Other cottids

Reports of diets of other sculpins in St. Georges Bay were not found. The following are general descriptions of the feeding of Cottidae species taken from Scott and Scott (1988). The grubb, *Myoxycephalus aeneus*, is a coastal fish associated mostly with estuaries in the Gulf of St. Lawrence. Diet is comprised of shrimp, crabs, sea urchins, copepods, snails, other molluscs, sea squirts, and many marine and estuarine fish such as cunner, eels, sand lance, mummichogs, silversides, sticklebacks and tomcod.

The shorthorn sculpin, *Myoxycephalus scorpius*, feeds on crabs, shrimp and sea urchins, as well as amphipods and gastropods in some locations, but will eat any food available. The mailed sculpin, *Triglops murrayi*, or Moustache sculpin, feeds on amphipods, mysids, and other crustaceans. The arctic hookear sculpin, *Artediellus uncinatus*, or snowflake sculpin, exists over a broad variety of substrates. There is no diet information as it is a poorly studied species.

AMMODYTIDAE

American sand lance *Ammodytes americanus*

The American sand lance is found over clean sandy bottoms, a distribution likely associated with the sand lance's unique predator avoidance behavior of swimming at full speed and embedding itself into the substrate, hence their name. Considering their importance as a trophic link between zooplankton and commercially important fish (Meyer et al., 1979), they are a poorly studied species. Deterrents in the study of this species is their avoidance behavior as described above and ability to escape and evade trawl net (Livingstone, 1962, cited in Meyer et al.,1979).

Meyer et al. (1979) studied the diet of American sand lance on the eastern boundary of Massachusetts Bay, in the Gulf of Maine. The vast majority of the Gulf of Maine diet is reported to be composed of copepods (Table 58); other prey includes amphipods, *(Calanus* sp., *Pseudocalanus* sp.), mysids, krill, (*M. Norvegica)*, salps, animal eggs, and arrow worms, which are significant by weight, but not by percent occurrence (present in 2.2% of stomach examined).

Diets of sand lance species of the Atlantic and Pacific oceans were compared by Reay (1970), who found them to be very similar, copepods, being the major prey. The diet of the American sand lance in Maine waters diverges from other reported diets in a lack of phytoplankton. This could certainly be a result of seasonal effects, or uniqueness of this population. Both the American sand lance and the northern sand lance (*Ammodytes dubius*), occur in eastern Canada. Because of the observed similarities of diet among many species and the questionable taxonomic distinction between the two

species (Meyer et al., 1979), diet data reported by Scott (1973b) of the northern sand lance from the Nova Scotia Banks is also presented in Table 58 for comparison.

Copepods are observed to be the largest diet component of the northern sand lance, although krill and polychaete larvae, and several small components are also consumed. As with the American sand lance, copepods are preyed upon most, while other invertebrates comprise the remainder of the diet.

Table 58: Stomach contents of American sand lance and northern sand lance in two North Atlantic sites.

	American sand lance Gulf of Maine, percent weight, Meyer et al. (1979)	Northern sand lance Nova Scotian Banks, percent volume*, Scott (1973b)
Polychaete larvae	.	14.88
Copepods	41.43	64.97
Amphipods	0.09	0.08
Mysids	0.32	.
Krill	0.41	13.68
Arrow worms	39.91	0.05
Salps	0.04	.
Animal eggs	<0.01	0.48
Trematodes	0.01	0.08
Crustacean larvae	.	2.88
Cirriped larvae	.	0.29
Larvaceans	.	2.56
Unidentified	17.79	.
No. stomachs	90	48.6
% empty	35.6	.

* some prey items less than 0.10 % not presented

AGONIDAE

Alligatorfish · *Asidophoroides monopterygius*

This fish is believed to be distributed throughout the St. Georges Bay Kenchington (1980). It is bottom-living, and is assumed to feed on small invertebrates (Scott and Scott, 1988). There was no published data found concerning its diet

STICHAEAIDAE · PRICKLEBACKS

Four pricklebacks species are found in the study area, these fish are bottom dwellers generally found over rocky substrate (Kenchington, 1980). They are carnivorous, feeding off crustaceans and marine invertebrates. The daubed shanny, *Lumpenus maculata,* feeds on annelid worms, amphipods and small crustaceans. The radiated shanny, *Ulvaria subbifurcata,* feeds on copepods, fish eggs, small fish, nereids, scale worms, and amphipods. The snake blenny, *Lumpenus lumpretaeformi,* is reported to feed on amphipods, copepods small starfish and molluscs in the North Sea (Scott and Scott, 1988). The Arctic shanny, *Stichaeus punctatus* is thought to be infrequent to St. Georges Bay (Kenchington, 1980). It feeds upon amphipods, polychaetes, isopods, mysids and ostracods, while the young feed on copepods and amphipods (Scott and Scott, 1988).

ACIPENCERIDAE

American Atlantic sturgeon · *Acipenser oxyrynchus oxyrynchus*

American Atlantic sturgeon are a benthic anadromous species, spending most of their lives in salt water. They have existed along the western Atlantic coast only at low numbers since the early 1900's because of intensive fishery. Of the two subspecies, the northern one resides in St. Georges Bay, and is more abundant and widely distributed than the southerly one (Smith, 1985).

Young sturgeons remain in fresh water, where they eat primarily plant and animal material from the bottom sediment with their protractile mouths (Smith, 1985). Johnston et al. (1997) examined the marine diet of sturgeon caught in a commercial fishery off the coast of New Jersey. Stomach contents by percent weight are presented in Table 59.

Spring sampling found isopods as the prey consumed in greatest quantities, while fall sampling found polychaetes to be the largest portion of sturgeon diet. Low values for fish prey were unexpected. A striking feature of these results is the average of 42.5% of the weight of stomach contents being sand or organic debris. This has been observed previously by Smith (1985) who believed it to be incidentally ingested, but Mason and Clugston (1993), cited by Johnston et al. (1997) suggest that it provides a source of nourishment via organic material and microbes. Smith (1985) reports marine diet components to include amphipods, isopods, shrimp, polychaetes, molluscs and small fish, especially sand lance.

The high percentage of empty stomachs was suspected to be the result of thorough digestion, or the mode of capture.

Table 59: Stomach contents of 275 Atlantic Sturgeon, collected off New Jersey coast; % by weight, seasonal data averaged from Johnston et al. (1997).

	Spring 1993, 1994	Autumn 1992, 1993
Hydrozoans	**0.1**	**9**
Nematodes	**0.2**	**< 0.1**
Polychaetes	**37.8**	**65.4**
Arthropods	**66**	**20.5**
Isopods	53.9	13.4
Amphipods	< 0.1	0.6
Decapods	12.1	6.2
Stomatopods	0	0.3
Molluscs	**0**	**3**
Bivalves	0	3
Echinoderms	**0**	**1.8**
Fish larvae	**1.6**	**0**

MYXINIDAE

Hagfish · *Myxine glutinosa*

The abundance of hagfish in St. Georges Bay is unknown, partly due to its inconspicuous nature (Kenchington, 1980). It dwells in soft-bottom sediments and is generally thought to scavenge dead and dying fish, however, Martini et al. (1997) suspect it to be a somewhat active predator. The hagfish produces slime so profusely that any predator might risk suffocation in trying to ingest one (Scott and Scott, 1988).

Martini et al. (1997) describe hagfish as opportunistic feeders and scavengers, which feed on polychaetes, herring, hermit crab, shrimp, and priapulids, and possibly pandalid shrimp. Hagfish is a notable prey of other species such as cod, halibut, hake, and harbour porpoise. Martini et al., (1997) suggest that hagfish may play a significant role in recycling the biomass of bycatch into the ecosystem.

CYCLOPTERIDAE

Lumpfish · *Cyclopterus lumpus*

The lumpfish primarily feeds on coelentrates, ctenophores, arrow worms, various crustaceans, small fishes, some molluscs and polychaetes (Gregory and Daborn, 1982). Adults spawn in subtidal and intertidal water and juveniles develop in the intertidal zone, although some have been found in pelagic waters. Juveniles in pelagic waters have been found to consume surface-feeding amphipods and copepods (Daborn and Gregory, 1983).

Lumpfish are thought only to feed in winter (Collins,1976). Summer studies of intertidal juvenile lumpfish in Maine were found to have a less varied diet than the adult, probably due to the restriction of a smaller mouth, as well as reduced prey spectrum in tidepools (Anonymous, 1987). The diet consists mostly of amphipods and isopods, but also copepods, cumaceans, polychaetes, mysids and *Acarina* sp. are significant by percent weight. The study in Maine was conducted during summer and did observe feeding in juveniles.

Other Cylopteridae

The Atlantic seasnail, *Liparis atlanticus* is an inshore benthic fish, feeding in shallow waters on crustaceans, polychaetes and plant material. The Atlantic spiny lumpsucker, *Eumicrotremus spinosus* is found over mud or gravel bottom, and feeds cheifly on amphipods. No information on the diet of the striped sea snail, *Liparis liparis* is available (Scott and Scott, 1988).

CRYPTACANTHIDAE

Wrymouth · *Cryptocanthodes maculatus*

The wrymouth is expected to occur in the St. Georges Bay, although none have been observed (Kenchington, 1980). These fish are an inshore intertidal bottom species that burrow into the mud, and feed on amphipods and mud shrimp (Scott and Scott, 1988).

LABRIDAE

Cunner · *Tautogolabrus adspersus*

The cunner is considered the most abundant inshore fish in St. Georges Bay. They are found over hard bottom and also among vegetation in the bay from May onwards. Cunner remain in the bay for winter, settling under rocks and becoming inactive (Kenchington, 1980). Their occurrence in large numbers makes them an important component of the St. Georges Bay ecosystem (T. Lambert, pers. comm.).

Cunner are found in areas of uneven bottom, and are a substantial food for fish and seabirds, where abundant. Cunners are small omnivores, feeding off benthic and near-bottom species such as molluscs, crustaceans, and perhaps sea squirts, fish eggs, eelgrass, barnacles, urchins, and sea worms in shallow inshore waters (Scott and Scott, 1988).

Additional diet items reported are blue mussels, barnacles, soft shelled clams, *Mya arensris*, amphipods, shrimps and small lobsters (Anonymous, 1989). Feeding is influenced by habitat as well as location and predator size class. Juveniles preferentially prey upon mussels, but shift to isopod consumption in the summer and fall, at which time feeding intensity declines (Anonymous, 1989).

PHOLIDAE

Rock gunnel · *Pholis gunnellus*

The rock gunnel inhabits intertidal habitat where it feeds on polychaetes, crustaceans and amphipods, as well as algae and insect larvae. It is frequently a food of cod, pollock and seabirds. Feeding ceases during the winter (Scott and Scott, 1988).

4. Seabirds and coastal waterfowl

Seabirds have an integral role as predators in the marine ecosystem. Studies on their influence on an ecosystem often address the degree to which particular species compete with commercial or recreational fisheries for the resource. Seabirds identified by Davis et al. (1999) within the St. Georges Bay ecosystem are as follows:

Inshore birds:

Great cormorant, *Phalocrocorax carbo*
Double-crested cormorant, *Phalocrocorax auritus*

Great black-back gull, *Larus marinus*
Herring gull, *Larus argentatus*
Iceland gull, *Larus glaucoides*

Common tern, *Sterna hirundo*
Arctic tern, *Sterna paradisaea*
Black guillemot, *Cephus gryle*

Offshore seabirds:

Gannet, *Morus bassanus*
Black-legged kittiwake, *Rissa tridactyla*

Figures of abundance of these birds specific to the study area are not available; Table 60 presents estimates of some of these species in area 4Tg, the Northwestern Atlantic Fisheries Organization (NAFO) unit area in which St. Georges Bay is located. This region includes Prince Edward Island and eastern Northumberland Strait, and is illustrated in Figure 2. Generally, the distribution of seabirds in 4Tg reflects their distribution in the southern Gulf. Inshore species, particularly gulls, are prevalent throughout the Gulf, but offshore seabirds are virtually absent from the southern Gulf. Cormorant distribution, in contrast, is concentrated in the southern Gulf and the St. Lawrence estuary (Cairns et al., 1991).

Table 60: Numbers of breeding pairs of seabirds estimated for 4Tg, Cairns et al. (1991).

	Breeding pairs of seabirds
Double-crested cormorant	735
Herring gull	1549
Great black-backed gull	892
Common tern	409
Arctic tern	2
Black guillemot	104

Seabird predation is reduced in the Gulf relative to the open ocean because of ice cover in the winter, low populations of offshore fish species and a depressed bird population due to human activity (Cairns et al., 1991).

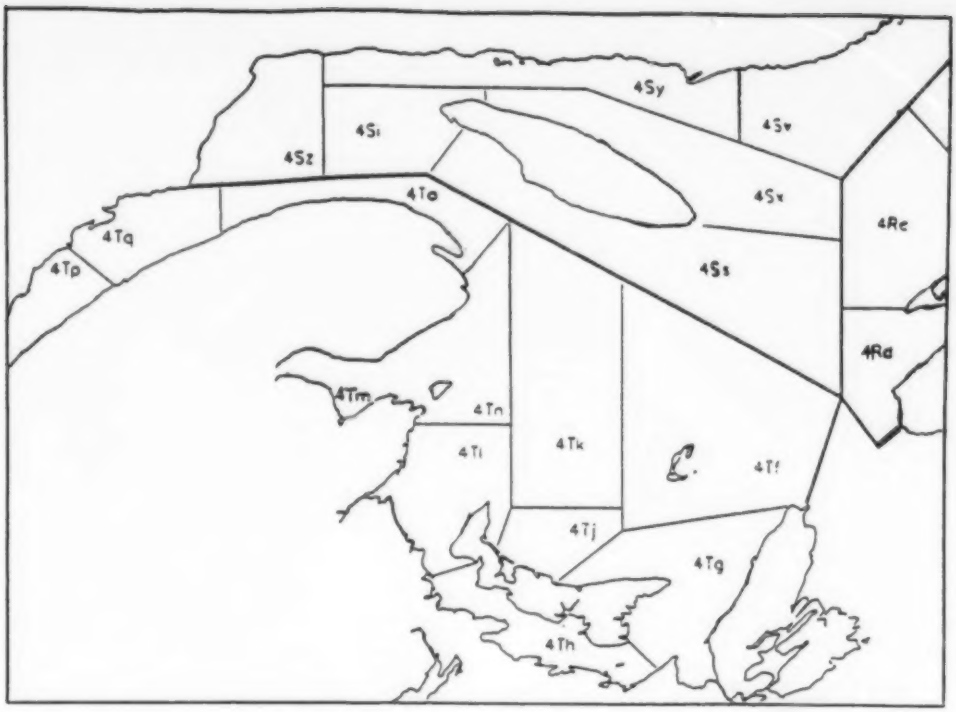

Figure 2: NAFO unit areas of the Gulf of St. Lawrence from Cairns et al. (1991).

Within the Gulf of St. Lawrence, Cairns et al. (1991) estimates that capelin and sand lance are most heavily preyed upon and identifies the southern Gulf as experiencing less intense predation, because of fewer cold water fish prey. Thus the impact of seabird predation for St. Georges Bay would be expected to be less than the estimated average removal rate of 0.04 g C/m^2/yr. Table 61 presents data from a series of cormorant diet studies from throughout the Gulf, compiled by Cairns et al. (1991), and also from Maine (Blackwell et al., 1995).

The data presents the overwhelming importance of groundfish, chiefly winter flounder and white hake to the double-crested cormorant population of 4Tg (encompassing the St. Georges Bay), as contrasted by a significant contribution of pelagic and schooling estuarine fish and crustaceans in other sample areas.

Great cormorants are strictly marine breeders (Cairns, 1998). Thus no salmonid species or freshwater fish were found in their diet, and only a small percentage of prey species were estuarine. Sand lance and herring are the largest pelagic fish prey components, but 79 % of the fish were marine bottom fish, including pollock, sculpins and flatfish.

Samples were collected either from stomachs of sacrificed birds or from regurgitant. Cormorant chicks and adults form regurgitated pellets, found in colonies,

Table 61: Diet of great and double-crested cormorants in the southern Gulf of St. Lawrence, Cairns et al. (1991), and Maine, Blackwell et al. (1995).

	Great cormorant	Double-crested cormorant		
	Magdalens 4Tf, Pilon et al. (1983)	Prince Edward Island, Cairns (1998)	Area 4Tg S. eastern Gulf Gallant (1988)	Maine, Blackwell et al. (1995)
Benthic Fish				
Winter flounder	.	.	35.4	.
Unidentified flatfish	34.1	7.02	.	.
Cunner	25.5	12.04	17.2	5.0
Sculpins	4.1	4.35	8.9	39.9
White hake	.	5.3	37.1	.
Blennoidea	5.5	0.4	.	.
White perch	.	5.02	.	.
Wrymouth	.	.	.	6.3
Rock gunnel	.	.	.	6.9
Estuarine fish				
American eel	.	3.74	1.4	1.9
Atlantic tom cod	.	-	.	0.7
Gaspereau	.	11.88	.	15.8
Rainbow smelt	.	22.69	.	0.8
Atlantic silverside	.	1.78		.
Sticklebacks	.	12.00	.	.
Pelagic Fish				
Atlantic herring	0.3	.	.	.
Sand lance	30.6	.	.	.
Crustaceans	.	**0.4**	.	**39.6**
Unidentified	.	.	.	4.5

that contain bones and otoliths used to identify prey (Cairns, 1998). Double- crested cormorants from the 4T area are reported by Cairns et al. (1991) to be reflective of the Gulf diet pattern, with flatfish and sculpins being large diet components. However, pelagic species such as capelin, sand lance and herring, were found to contribute significantly to cormorant diet in other Gulf, and southern Gulf studies.

Double-crested cormorants are known to feed in estuarine and fresh water ponds Cairns (1998) noted an increase of salmon smolts in cormorant diet during the salmon runs in Atlantic sites. Seventy-three percent of fish eaten were commercial or recreational species during the smolt run. Birds were found to concentrate at 'run' sites at that time, and sampling was concentrated in areas known for salmon population, thus this data is biased as a result. Of the prey species, 16 % were marine prey. Sampling

done at times other than the smolt run revealed diet composition of which 23 % was estuarine/diadromous. Marine pelagic species constituted 14% and 55 %; species such as cunners, sculpins, cod, pollock, flounder, and blennoids were among those preyed upon.

Eastern New Brunswick tern diets described by Chapdelaine et al. (1985) were considered by Cairns et al. (1991) to be representative of fish/invertebrate prey ratios in the southern Gulf diet. Chapdelaine et al. (1985) found fish (sand lance and capelin) to comprise 65 % of the tern diet. Pelagic invertebrates constituted 36 % and 41 % of diets for common and arctic terns, respectively (Table 62). Mills (1957) examined the impact of common tern and herring gull predation on lobster larvae in western Northumberland Strait, as seabird predation was thought at the time to be a significant contributor to their heavy mortality rate. Of the 15 terns examined, percent occurrence of insects, fish, crustaceans and annelids were 76.9, 69.2, 23.1, and 7.7 %, respectively. Crustaceans consumed were chiefly pelagic forms, and just one larval lobster was found at a time when lobster larvae were abundant in the waters of the study area.

Black guillemot diet components presented in Table 62 by Cairns et al. (1991) was collected from guillemot chicks, as adult data was not available for the Gulf. This data under-represents the amount of crustaceans consumed, which are a larger part of the adult's diet. Oceanic species, particularly benthic arctic shanny and rock gunnel were found to be consumed in large quantities. The northern gannet diet was composed largely of mackerel, and sand lance (Table 62).

Table 62: Diet of the common tern, arctic tern, black guillemot and northern gannet in the Gulf of St. Lawrence.

	Common tern Chapdelaine et al. (1985)	Arctic tern Chapdelaine et al. (1985)	Black guillemot Cairns et al. (1991)		Northern gannet, 4Tf Burton(1980), and Cairns, unpublished
	4Sy	4Sy	4Sv	4Tp	
Benthic Fish					
Sculpins	.	.	.	24	.
Blennoidea	.	.	55.3	46	.
Estuarine fish					
Atlantic tom cod	.	.	35.1	8	.
Pelagic Fish					
Atlantic herring	.	.	.	.	**0.9**
Sand lance	42	51	8.5	8.0	37.5
Capelin	22	8	.	15	
Atlantic mackerel	.	.	.	.	52.4
Atlantic saury	.	.	.	.	8.1
Squid	.	.	.	.	**1.1**
Crustaceans	**36**	**41**	**1.1**	.	.

Gulls are omnivores, consuming fish, marine invertebrates, fish offal, and terrestrial food (Cairns et al.,1991). Little information on diet is available for the Gulf area. Cairns et al. (1991) estimated fish to comprise 50 % of herring and great black-backed gull diets, 30 % non-marine food, 10 % benthic invertebrates, and 10 % fish offal. Mills (1957) found that of thirty-one herring gull stomachs collected from western Northumberland Strait, 35.5 % contained only shell fragments of crustaceans, and no lobster larvae (Table 63).

A study of the diet of three gull species collected mainly from islands near St. John's, Newfoundland (Threlfall, 1968) are presented in Table 63. Here, most herring gulls consumed plant material, fish being second most commonly found, whereas fish was found in the largest number of great black-backed gull and kittiwake stomachs.

Cairns et al. (1991) present estimates of fish consumed by seabird predation within areas of the Gulf of St. Lawrence (Table 64). Consumption by the seabird population within 4Tg is weighted toward benthic prey. Cairns et al. (1991) also point out that the absence of data from waterfowl predation causes these figures to be significant underestimates of consumption, however, they note that harvest by seabirds is small compared to the commercial landings of 29,616 tonnes of fish for that area.

Consumption of marine species by waterfowl is significant in the St. Lawrence estuary in both summer and winter, and there is some information compiled on winter waterfowl diet in that area (Guillemette et al., 1992; 1996) Ice cover in the southern Gulf prevents the overwintering of waterfowl in the study area, and therefore confines predation to the period of spring through fall. There are breeding populations of waterfowl within St. Georges Bay, but there are no diet studies known (N. Seymour, pers. comm.). The estuaries of St. Georges Bay do provide staging grounds for large numbers of migratory waterfowl (Seymour, 1997), which would impact the food web seasonally. Benthic invertebrates are the major prey of sea ducks (Goudie and Ankney, 1976, cited in Cairns et al., 1991).

The time frame of this report did not allow investigation of size or species constituting the waterfowl population in St. Georges Bay.

Table 63: Percent occurrence of prey items in stomachs of herring and great black-backed gulls and black-legged kittiwakes.

	Herring gulls Threlfall (1968)	Herring gulls Mills (1957)	Great black-backed gulls Threlfall (1968)	Black-legged kittiwakes Threlfall (1968)
Seeds, berries	3.24	.	3.77	-
Vegetation	32.64	19.4	20.75	14.29
Annelids	0.24	.	1.89	-
Arthropods				
Insects	7.41	67.7	1.89	-
Crustaceans	0.11	35.5	-	1.79
Molluscs	9.84	.	3.77	4.46
Echinoderms	0.58	.	1.89	0.89
Fish	22.8	25.8	33.96	41.08
Birds		12.9		
Pieces	3.36	.	5.66	-
Eggs	0.93	.	-	0.89
Miscellaneous	14.00	19.4	16.98	25.71
No. stomachs	401	36	31	69
Percent empty	4.86	13.8	9.44	10.71

Table 64: Estimated fish harvest (tonnes) by seabirds from Area 4Tg (Cairns et al., 1991)

Prey group	Prey harvest
Benthic, estuarine fish	**949**
Flatfish	404
Cunner	226
Sculpins	67
White hake	144
Blennoidea	55
Other estuarine fish	13
Pelagic Fish	**245**
Atlantic herring	2
Sand lance	241
Small pelagics	1
Fish unclassified	**279**
Benthic invertebrates	**54**
Pelagic crustaceans	**4**
Total living prey	**1532**

5. Marine mammals

5.a. PINNIPEDS · SEALS

The three species of pinnipeds in St. Georges Bay are the hooded seal, *(Cystophora cristata),* harbour seal *(Phoca vitulina)* and grey seal *(Halichoerus grypus)* (Kenchington, 1980). The importance of seals within the ecosystem has been a subject of high profile since the decline of the groundfish fishery of the Northwest Atlantic. The predatory impact was thought by some to be a critical factor in the declining fish population. The harp seal, which is not reported to be found in St. Georges Bay, has received a great deal of attention, as it was the most abundant seal in Atlantic Canada (Hammill and Stenson, 1997). Population estimates of seal species for all Atlantic Canada are presented in Table 65.

Table 65: Estimated population size (numbers of individuals) for seal species in Atlantic Canada, Hammill and Stenson (1997).

	1991	1996
Harp seal	4,200,000	5,200,000
Hooded seal	470,000	627,000
Grey seal	97,000	173,000
Harbour seal	23,000	32,000

Prey consumption estimates for seals in the southern Gulf region (Hammill and Stenson, 1997) are presented in Table 66. Grey seals have, by far, the greatest predatory impact, followed by the harbour seal. Hammill and Stenson (1997) did not consider hooded seals to have a significant presence in the southern Gulf and therefore did not present an estimate for their consumption. Because they are known to occur in St. Georges Bay, it could be assumed that the feed on some prey.

Table 66: Estimated prey consumption (tonnes) by 3 seal species in the southern Gulf of St. Lawrence, 1996. Hammill and Stenson (1997).

	Fish	Invertebrates	Total prey
Grey seal	40,429	1,245	41,674
Harbour seal	361	97	458
Hooded seal	0	0	0

Diet studies of seal populations rely heavily on identification of prey species by the persistence of otoliths. Otoliths of different prey species are digested at differential rates. The implications of this is that those fish which produce more fragile otoliths, such as herring, will be underestimated. In addition, seals have been demonstrated in captivity to accumulate squid beaks in their stomachs, therefore over-representing the number of squid eaten (Bowen and Harrison, 1996).

Studies reviewed typically report approximately half of the stomachs as empty. Murie and Lavigne (1992) suggest that this indicates that seals possibly do not feed every day.

Grey seal · *Halichoerus grypus*

The grey seal population of Eastern Canada migrates to southern Gulf of St. Lawrence ice flows and Sable Island to give birth from late December to February and then disperses to feeding areas throughout the Gulf, Scotian Shelf and Newfoundland (Benoit and Bowen, 1990a). A significant amount of work was done on the diet of Grey seal, as it is the definitive host of the sealworm, *Pseudoterranova decipiens*. This sealworm parasitizes fish muscle, thus has significant impact on the commercial fishery sector. The grey seal is also implicated as a competitor with commercial fisheries for the fishery resource, and a source of revenue loss through damaged gear (Benoit and Bowen,1990b).

Diet of grey seals in the southern Gulf was found by Bowen and Benoit (1990a) to consist of skates, flatfishes, herring, cod and rainbow smelt, making up 70 % of prey occurrences. Table 67 presents their findings in frequency of occurrence. Grey seals were found to consume predominantly groundfish. Benoit and Bowen (1990a) found an increase in consumption of pelagic prey that were returning from deep water early in the spring. This phenomenon has been interpreted by Mansfield and Beck, (1977) as a seasonal utilization of species locally abundant in the summer, while maintaining a primary year-round reliance on ground fish. More recent data suggests a greater importance of migratory species as prey. Because feeding is found to be greatly reduced during breeding season (Boness and Jamieson, 1979), seals are thought to rely on consuming high energy sand lance, herring and silver hake to replenish energy reserves.

Grey seals are opportunistic feeders; the presence of rocks and mud in stomach contents indicate persistent foraging in the benthos. The geographical variation in abundance of pelagic prey species is reflected in the seal diet, further supporting the assertion that an opportunistic feeding strategy is utilized. Feeding in the northern Gulf reflected summer feeding patterns at Anticosti Island (Benoit and Bowen, 1990b), where seals relied heavily on schooling or grouped fish, observed as many seal stomachs containing just one or two fish types (Murie and Lavigne, 1992).

Benoit and Bowen (1990b) reported most frequent prey of Anticosti Island grey seals to be capelin, cod, herring, lumpfish and flatfish, accounting for 72 % of prey items (Table 68). Cod was most important by weight, contributing 41.5 % of the stomach content mass; capelin and herring contributed less than 10 % of the mass of prey. Murie and Lavigne (1992) found cod contributing 13 % wet mass of seal diet in the northwestern Gulf. Invertebrate prey were found in small quantities and suspected to be present as prey of consumed prey. Invertebrates as prey occurred at a 22 % incidence in the northwestern Gulf of St. Lawrence grey seal diet, but these constituted <1 % of the prey mass.

Table 67: Frequency of occurrence of prey items in grey seal stomachs collected in the Southern Gulf of St. Lawrence, 1986 and 1987, Benoit and Bowen (1990a).

Prey group	% occurence
Fish	**84.9**
Capelin	-
Cod	13.5
Herring	21.5
Flatfishes	27
Mackerel	1.1
Skate	30.3
Skate eggs	4.5
Hake	3.4
Gaspereau	2.2
smelt	5.6
Salmon	2.2
Sculpin	2.2
Unidentified	25.8
Invertebrates	**14.1**
Squid	4.5
Crab	7.9
Shrimp	4.5
Clam	2.2
Sippunulia	2.2
Lobster	1.1
Mussel	1.1
Seaweed	1.1
Groundfish	**29.1**
Pelagic	**14.2**
Other finfish	**25.5**
Invertebrates	**14.9**
Unidentified	16.3
No. stomachs	194
Empty stomachs	105

Hammill and Stenson (1997) report sand lance as the prey species consumed in the largest quantities, contributing 45.1 % by weight to the grey seal diet, whereas cod comprises 19.2 % and lumpfish and flatfish represent 7.5 % and 7.4 % respectively (Table 68).

At Anticosti Island, seal predation was characterized as focussing on young, schooling or aggregated fish. Seventy-two percent of the stomachs in this study contained just one prey species and prey length was concentrated within a 20-30 cm range for cod, plaice, herring, and lumpfish, although average length for other species varied from 13.9 to 32.6 cm. No correlation was found between seal size and length of cod prey. Sizes of

Table 68: Diet components of 295 grey seals of Anticosti Island (1982, 1983, 1986, 1987), expressed as percent frequency and percent weight of stomach contents (Benoit and Bowen, 1990b) and percent wet weight of southern Gulf grey seals (Hammill and Stenson, 1997).

	Anticosti Island Benoit and Bowen (1990b)		Hammill and Stenson (1997)
	% frequency	% weight	% weight
Capelin	38.6	6.6	1.2
Cod	29.3	41.5	19.2
Herring	23.9	3.7	7.5
Lumpfish	13.6	14.3	1.5
Ocean pout	4.3	16.4	1.1
Flatfishes	10.9	5.3	7.4
Mackerel	8.2	4.5	4.3
Haddock	1.1	2.9	0.2
Salmon	0.5	2.7	0.2
Gr. Halibut	1.1	0.7	-
Hake	1.1	0.5	3.2
Pollock	1.1	< 0.1	0.9
Cunner	0.5	0.4	-
Wolfish	0.5	0.2	1.2
Sculpin	0.5	0.1	0.2
Sand lance	.	.	45.1
Squid	.	.	3
Other	.	.	3.6

cod and herring prey do not overlap with those taken by the commercial fishery (Murie and Lavigne, 1992; Benoit and Bowen, 1990b).

Grey seal would seem to compensate for variability in caloric content when feeding, as cod, a less calorie-rich prey is consumed at a higher percent body weight than is capelin (1.5% compared to 0.8%). These proportions of the prey mass are calculated to be equivalent in terms of caloric value by Benoit and Bowen (1990b). Males were found to consume more food than females, this was attributed to the difference in size between the sexes (Benoit and Bowen, 1990b).

Benoit and Bowen (1990b) report a reduction of diversity of prey with age, and demonstrated the variation of diet over years, but discounted change in prey abundance as the cause, as consumption changed during a period when prey population size did not. An inverse relation was also observed between consumption of herring and capelin in the grey seal population off Anticosti Island.

Harbour seal · *Phoca vitulina*

Boulva and MacLaren (1979) found the most frequent prey groups of harbour seals along the Atlantic coast and within the Gulf of St. Lawrence to be Atlantic herring, squid, flounder (chiefly winter flounder), alewife and hake (Table 69).

Table 69: Percent frequency of prey items in stomachs of harbour seals in the Gulf of St. Lawrence (Boulva and McLaren, 1979).

	% frequency occurrence
Atlantic herring	24.2
Squid	20.6
Flounders	14.1
Alewife	6.8
Hake	6.0

Bowen and Harrison (1996) examined the diet of harbour seals within the Bay of Fundy and off northeastern Nova Scotia, choosing these sites for their similarity in habitat, but known differences in fish assemblages. Variation in proportions of prey types between the two sites reflected the differences in abundances of prey and was therefore thought to result from this variation (Table 70). Atlantic herring and squid consumption were equivalent in the two sites, but Atlantic cod was dominant in the Bay of Fundy while pollock was a more prominent diet component on the Atlantic.

Atlantic herring, Atlantic cod, pollock and short-finned squid contributed 84 % by mass of harbour seal diet. As with grey seals, harbour seals prey upon a staple of groundfish and have geographically varied diets depending on the local abundance of small schooling species. However, these two seal species display differences in diet within the same habitat that indicate that differences in foraging behavior exist.

Diet was notably different in seal pups. Pelagic species, such as herring and squid were the main prey, but after one year, diet was composed of more bottom feeders such as gadoids, and flatfish. The yearling diet included a composite of the two diets. The difficulty of identifying and diving for benthic prey for young seals may contribute to this difference (Bowen and Harrison, 1996).

Increased prey size with predator size was observed for cod prey in the Bay of Fundy. Average lengths of prey varied slightly by site, but for major prey species ranged from 17 to 35 cm, although length of cod prey reached 55 cm in the Bay of Fundy.

Table 70: Food of harbour seals collected from the Bay Fundy and the northeastern Nova Scotian coast from 1988 to 1992, percent mass (Bowen and Harrison, 1996).

	Bay of Fundy	Atlantic Coast
Atlantic herring	29.7	30.2
Atlantic cod	21.5	11.1
Squid	20	18.1
Winter flounder	7.2	0.4
Alewife	6.9	0.8
Hake	4.9	0.5
Pollock	4.6	32.8
Mackerel	1.8	3.3
Ocean Pout	1.7	-
Silver hake	1.2	0.4
Redfish	0.3	0.1
Blueback herring	0.2	-
Haddock	0.1	0.1
Capelin	-	2.3
No. stomachs	164	85

Hooded seal *Cystophora cristata*

Limited information is available on the diet of the hooded seal in Eastern Canada. The hooded seal population was significantly depleted by a commercial harvest such that the species was fully protected in 1972. The population is presently increasing (Hammill et al., 1997) but Hammill and Stenson (1997) consider this seal's importance to be restricted to eastern and southern Newfoundland. Estimates by Hammill and Stenson (1997) of consumption in the southern Gulf of St. Lawrence were nil, but the presence of hooded seals in St. Georges Bay and their increasing population in the southern Gulf warrant discussion of their feeding habits.

Hooded seals oversummer in the Atlantic and enter the Gulf of St. Lawrence in the fall. Whelping occurs in March, the main location being to the north of Prince Edward Island (Hammill et al., 1997). The seals leave the Gulf in May. Diet composition in Newfoundland by percent weight was developed by Ross (1993) and presented in Hammill and Stenson (1997). Table 71 presents values for inshore and offshore consumption. Greenland halibut and redfish are both species which are not believed to be present in St. Georges Bay, but are observed as prominent in hooded seal diet. Fish resident to the bay which constitute large proportions of the hooded seal diet are Atlantic cod and flatfish.

Table 71: Estimates of hooded seal diet, percent wet weight, Hammill and Stenson (1997).

	Inshore	Offshore
Atlantic cod	1.2	10.1
Herring	14	-
Capelin	0.3	0.9
Witch flounder	-	15.5
Greenland halibut	42.2	31.6
Redfish	20.6	3.3
Flatfish	-	8.3
Squid	7.2	12.6
Arctic cod	14.5	-
Grenedier	-	5.7
Blue hake	-	4.2
Lancetfish	-	1.6
Eelpout	-	0.4
Other fish	-	5.8

5.b. CETACEANS - WHALES AND PORPOISES

The following is a list of cetaceans known or believed to occur in St. Georges Bay taken from Davis et al. (1999).

Minke whale, *Balaenoptera acutostrata* - has been identified by stranding at Tracadie, St. Georges Bay.

The cetaceans listed below have been stranded on adjacent coastline along the Northumberland Strait, although the portion of the time these species are in the bay is unknown.

Fin whales, *Balaenoptera physalus*
Sperm whales, *Physeter macrocephalus*
Long-finned pilot whales, *Globicephala melas*
White-beaked dolphins, *Lagenorhynchus albirostris*
Atlantic white-sided dolphin, *Lagenorhynchus acutus*
Harbour porpoise, *Phocoena phocoena*

The following are suspected to occur within the bay because of prevalence in nearby areas:

Blue whale, *Balaenoptera musculus*
Beluga, *Delphinapterus leucas*

The importance of whales and dolphins within the St. Georges Bay ecosystem has not been documented. Kenney et al. (1995) presents the considerable difficulties associated with trophic analysis of whales. Metabolism and weight are difficult to quantify in such large animals. In addition, diet analysis based on stomach contents is restricted to stranding, as they are legally protected animals.

Whale species which are not harvested are limited by food resources as they are not preyed upon within their ecosystem. Without control of population size, it can be argued that they are, or will eventually be placed in indirect, or direct competition with fisheries for resources. Much of their diet is composed of different species or ages than those utilized by fishery, but, in particular, herring and mackerel are exceptions to this. Kenney et al. (1995) suggests that predation may have delayed recovery of herring stocks on Georges Bank. They illustrate the close linkage of the fishery and whale population in the utilization of the fish resource by reporting the coincidence of the decline in the offshore capelin population in Newfoundland with an increase in inshore humpback entanglement and mortalities in codtraps.

Whales and dolphins are significant prey consumers on the northeastern United States shelf system and are thought to be much more important than previously believed in terms of competition for commercially significant fish. Cetaceans were estimated to be taking more than twice the 1995 commercial fishery harvests in that region and are

thought to require 10.3 % of the total primary production. These values are derived from models developed by Kenny et al. (1995) and should be understood to be approximate.

The diets of cetaceans identified as present or likely present in the St. Georges Bay have not been examined to any extent. Details of harbour porpoise diet in the Bay of Fundy and Maine have been published, and will be discussed. Diet specifics of cetaceans along the U. S. northeast continental shelf have been reviewed (Kenney at al., 1995) and information concerning relevant species are presented in Table 72. This information gives a general idea only of what they may be expected to eat in any specific area.

Table 72: Diet trends in selected cetaceans in the northeastern American shelf system, percent biomass, Kenney et al. (1995).

	Fish	Squid	Zooplankton
Fin whale	90	-	10
Long-finned pilot whale	10	90	-
Sperm whale	20	80	-
Minke whale	95	-	5
Atlantic white-sided dolphin	90	10	-
Harbour porpoise	95	5	-

The discussion to follow of the general diet components in the northern hemisphere of relevant cetaceans is taken from Evans (1987). Baleen whales tend to feed by 'gulping' or 'skimming' and filtering out the abundance of small organisms in marine waters. These species exhibit seasonal and geographical variations in diet, chiefly feeding on krill, but also small fish and squid, depending on availability of plankton, which may vary considerably throughout the year. Blue whales feed almost exclusively on the krill *Thysanoessa, Nematoscelis* and *Meganysitiphanes*, and copepods, chiefly *Temora*. The fin whale feeds on *Thysanoessa, Meganysitiphanes*, and krill; the copepod *Calanus*, as well as herring, capelin, sand lance, cod, pollock, sardine, walleye pollock and various lanternfish. The minke whale feeds on herring, cod, capelin, *Eleginus*, navaga, polar cod, pollock, sand lance, krill, and pteropods.

Toothed whales feed mainly on schools of fish and squid, these prey being more prominent inshore and offshore, respectively. Pilot whales feed mainly on squid (Evans, 1987). The movements of long-finned pilot whales are known to follow those of short-finned squid in eastern Newfoundland. Cod, mackerel, pollock, eel, hake, Greenland halibut, white hake, sprat, hake, and scads are common prey of this whale. The diet of sperm whales includes squid, redfish, skate, cod, anglerfish, lumpsuckers and hagfish.

The beluga whale is an opportunistic feeder, thus has a varied diet geographically, feeding extensively on capelin, sand lance and squid in the St. Lawrence River; crustaceans, gastropods and possibly nereid worms are also eaten.

White-beaked dolphins feed on cold water prey, including cod, herring, silver hake, mackerel, capelin, and haddock, also octopus and squid, and sometimes benthic

crustaceans. The white-sided dolphin, which tends to have the same distribution as the former, feeds similarly, except moreso on offshore species. Blue whiting, cod, mackerel, smelt, herring, hake, squid and gammarid copepods are diet items.

Regional studies of harbour porpoise will be discussed in detail, however, general prey selection includes herring, sand lance, sprat, mackerel, sardine, blue whiting, poor hake, whiting, pollock, scads and cod.

Pauly et al. (1998) present standardized diet compositions for many marine mammals (Table 73), including all those of the St. Georges Bay. This is a compilation of worldwide data, and is therefore limited in relevance by the sources from which it was collected. Numerical trophic levels developed by Pauly et al. (1998) are assigned to prey groups, as well as species of cetaceans. These provide a perspective on their respective roles in the ecosystem.

Table 73: Standardized diets of cetaceans, percentage weight or volume (Pauly et al., 1998).

	Benthic inverte-brates, 2.2 bivalves, gastropods, octopus and echinoderm	Large Zooplank-ton, 2.2 crustaceans (krill)	Small squid 3.2	Large squid 3.7	Small pelagic fish, 2.7 clupeoids, scombroids	Meso-pelagic fish 3.2 lanternfish	Misc. 3.3 demersal gadoids, perciforms and anadromous	Trophic levels
Long-finned Pilot whale	-	-	40	35	-	-	25	4.4
Sperm whale	5	-	10	60	5	5	15	4.4
White-beaked dolphin	5	-	15	5	15	-	60	4.2
White-sided dolphin	10	-	15	10	15	10	40	4.1
Harbour porpoise	5	-	10	10	30	-	45	4.1
Beluga whale	20	-	5	5	20	10	40	4
Fin whale	-	80	5	-	5	5	5	3.4
Minke whale	-	65	-	-	30	-	5	3.4
Blue whale	-	100	-	-	-	-	-	3.2

Harbour porpoise · *Phocoena phocoena*

The harbour porpoise is a common predator in temperate coastal waters (Recchia and Read, 1989). Concern has been expressed over the degree to which they compete with the commercial fishery for the fishery resource. There is also concern over the impact of by-catch, as the Fundy population is suspected to be threatened by incidental catch (Gaskin, 1992). It is believed that harbour porpoise become tangled in cod nets when foraging for herring and capelin, rather than cod. No documentation of porpoise diet in the southern Gulf was located.

All studies reviewed identify the largest overall prey group as herring (Recchia and Read, 1989; Gannon et al., 1998; Fontaine et al., 1994) although there is some local variation. Table 74 presents data from these reports. In addition to herring, capelin, mackerel, cod and hake are also consumed in large quantities, depending on location.

Table74: Stomach contents of harbour porpoise in the Gulf of St. Lawrence, Gulf of Maine and the Bay of Fundy.

	Western Gulf 1989 Fontaine et al., (1994) % mass	Gulf of Maine 1989-1994 Gannon et al., (1998) % mass	Bay of Fundy, 1969-1972 Recchia and Read (1989) % proportion	Bay of Fundy, 1985-1986 Recchia and Read (1989) % proportion
Capelin	37.6	-	-	-
Herring	43	44	51.5	38
Redfish	10.3	<1	1	0
Mackerel	7	1	12.4	0.9
Atlantic cod	1.4	-	14.8	33.7
Squid	0.6	< 1	0.5	0.9
Pearlsides	-	3	-	-
Sand lance	0.5	-	-	-
Silver hake	-	22	-	-
Hake	-	26	0	4.3
Pollock	-	2	1.5	0
Haddock	-	-	4	0
American smelt	-	-	2	0
No. stomachs	138	95	26	27

In the western Gulf of St. Lawrence 66 % of the stomachs contained a single species, suggesting feeding on schooling fish. Herring, capelin and redfish were the largest prey groups here, the former two contributing 80 % of the caloric value of the diet. Among western Gulf study locations, herring and capelin showed varying importance; harbour porpoise of the Baie des Chaleurs alone fed more upon herring than capelin. Mean size of cod preyed upon are below the size taken commercially, but herring and capelin prey are generally large enough to be commercially fished (Fontaine et al., 1994).

The importance of capelin to the harbour porpoise is apparently unique within the region to the Gulf of St. Lawrence, as it is not reported in the other studies. Atlantic herring and hake were consumed in large proportions in the Gulf of Maine.

Recchia and Read (1989) observed differences in inshore and offshore diets and suggested that this reflected prey distribution. Crustaceans and polychaetes were found exclusively in porpoise that had consumed juvenile herring, and their presence was attributed to the diet of the herring, rather than that of the porpoise.

Analysis of the diet of the Maine population illustrated distinct changes in diet with age. Young calf diets consisted of 53 % by weight of pearlsides, and 11 % herring, compared to 3 % pearlsides and 44 % herring of the whole sample set. Herring and hake prey size of calves is smaller than prey size of adult porpoises (Gannon et al., 1998).

The reproductive cycle of harbour porpoises is such that after maturity (usually three years), females will reproduce yearly and will often be lactating while pregnant. This constitutes a greater need for prey. Recchia and Read (1989) found that lactating females ingested the same variety and size of fishes, but in greater numbers than males. Gannon et al. (1998) found a greater proportion of hake in lactating females.

Seasonal variation was evident in the increased prevalence of herring in the harbour porpoise fall diet relative to the summer (Gannon et al., 1998). The change in diet may reflect differences in prey abundance or seasonal movements of the porpoise which is perhaps required in order to meet their high energy requirements.

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Appendix 1: List of fish species occuring in St. Georges Bay (Davis et al., 1999).

Family	Species	Scientific Name
Acipenseridae	American Atlantic sturgeon[2]	*Acipenser oxyrhyncus*
Agonidae	Alligatorfish	*Aspidophoroides monopterygius*
Ammodytidae	American sand lance	*Ammodytes americanus*
Anguillidae	American eel	*Anguilla rostrata*
Atherinidae	Atlantic silverside	*Menidia menidia*
Bothidae	Windowpane	*Scophthalmus aquosus*
Charchariidae	Blue shark[2]	*Prionace glauca*
Clupeidae	Alewife	*Alosa pseudoharengus*
	American shad	*Alosa sapidissima*
	Atlantic herring	*Clupea harengus*
	Blueback herring	*Alosa aestivalis*
Cottidae	Arctic hookear sculpin[1]	*Artediellus uncinatus*
	Atlantic sea raven	*Hemitripterus americanus*
	Grubby	*Myoxocephalus aeneus*
	Longhorn sculpin	*Myoxocephalus octodecemspinosus*
	Mailed sculpin[1]	*Triglops murrayi*
	Shorthorn sculpin	*Myoxocephalus scorpius*
Cryptacanthidae	Wrymouth	*Cryptacanthodes maculatus*
Cyclopteridae	Atlantic seasnail	*Liparis atlanticus*
	Atlantic spiny lumpsucker[1]	*Eumicrotremus spinosus*
	Lumpfish	*Cyclopterus lumpus*
	Striped seasnail[1]	*Liparis liparis*
Cyprinodontidae	Mummichog	*Fundulus heteroclitus*
Gadidae	Atlantic cod	*Gadus morhua*
	Fourbeard rockling	*Enchelyopus cimbrius*
	Pollack	*Pollachius virens*
	Silver hake	*Merluccius bilinearis*
	White hake	*Urophycis tenuis*
Gasterostidae	Black-spotted stickleback	*Gasterosteus wheatlandi*
	Fourspine stickleback	*Apeltes quadracus*
	Ninespine stickleback[1]	*Pungitius pungitius*
	Threespine stickleback	*Gasterosteus aculeatus*
Labridae	Cunner	*Tautogolabrus adspersus*
Lamnidae	Porbeagle[2]	*Lamna nasus*
Molidae	Ocean sunfish[2]	*Mola mola*
Myxinidae	Hagfish[1]1	*Myxine glutinosa*
Osmeridae	American smelt	*Osmerus mordax*
	Capelin	*Mallotus villosus*
Petromyzontidae	Sea lamprey[1]	*Petromyzon marinus*
Pholidae	Rock gunnel	*Pholis gunnellus*

Appendix 1 (con't).

Pleuronectidae	American plaice	*Hippoglossoides platessoides*
	Smooth flounder	*Liopsetta putnami*
	Winter flounder	*Pseudopleuronectes americanus*
	Witch flounder	*Glyptocephalus cynoglossus*
	Yellowtail flounder	*Limanda ferruginea*
Rajidae	Little skate	*Raja erinacea*
	Thorny skate	*Raja radiata*
	Winter skate	*Raja ocellata*
Salmonidae	Atlantic salmon	*Salmo salar*
	Brook trout	*Salvelinus fontinalis*
Scomberesocidae	Atlantic saury	*Scomberesox saurus*
Scombridae	Atlantic bonito[2]	*Sarda sarda*
	Atlantic mackerel	*Scomber scombrus*
	Bluefin tuna	*Thunnus thynnus*
Stichaeaidae	Daubed shanny	*Lumpenus maculatus*
	Arctic shanny[1]	*Stichaeus punctatus*
	Radiated shanny	*Ulvaria subbifurcata*
	Snake blenny	*Lumpenus lumpretaeformis*
Stromateidae	Butterfish[1]	*Peprilus triacanthus*
Syngnathidae	Northern pipefish	*Syngnathus fuscus*
Xiphidae	Swordfish[2]	*Xiphias gladius*
Zoarcidae	Ocean pout	*Macrozoarces americanus*
	Vahl's eelpout[2]	*Lycodes vahlii*

1 Not conspicuous and not easily sampled, although possibly regularly occurring.
2 Uncommon, rarely seen.

Appendix 2: Scientific names of fish prey species discussed that do not occur in St. Georges Bay. Classification (if available) from Scott and Scott (1988).

Anchovy	Engraulidae
Argentines	Argentinidae
Atlantic menhadden	*Brevoortia tyrannus*
Barracudina	Paralepididae
Blue hake	*Antimora rostrata*
Blue whiting	*Micromesistius poutassou*
Bluefish	*Pomatomus saltatrix*
Duckbill barracudina	*Paralepsis atlantica*
Eelpout	*Melanostigma atlanticum*
Greenland halibut	*Reinhardtius hippoglossoides*
Grenedier	Macrouridae
Atlantic halibut	*Hippoglossus hippoglossus*
Haddock	*Melanogrammus aeglefinus*
Lancetfish	Alepisauridae
Lanternfish	Myctophidae
Pearlsides	*Maurolicus muelleri*
Polar cod	*Brosme brosme*
Red hake	*Urophycis chuss*
Redfish	*Sebastes* sp.
Sardine	*Clupea harengus harengus*
Scad	Carangidae
Scorpionfish	Scorpaenidae
Scup	*Stenotomus chrysops*
Snake mackerel	Gempylidae
Striped bass	*Morone saxatilis*
Tomcod	*Microgadus tomcod*

Appendix 3: Biomass estimates (tonnes) for fish collected by bottom trawl from St. Georges Bay, 1978, Kenchington (1980).

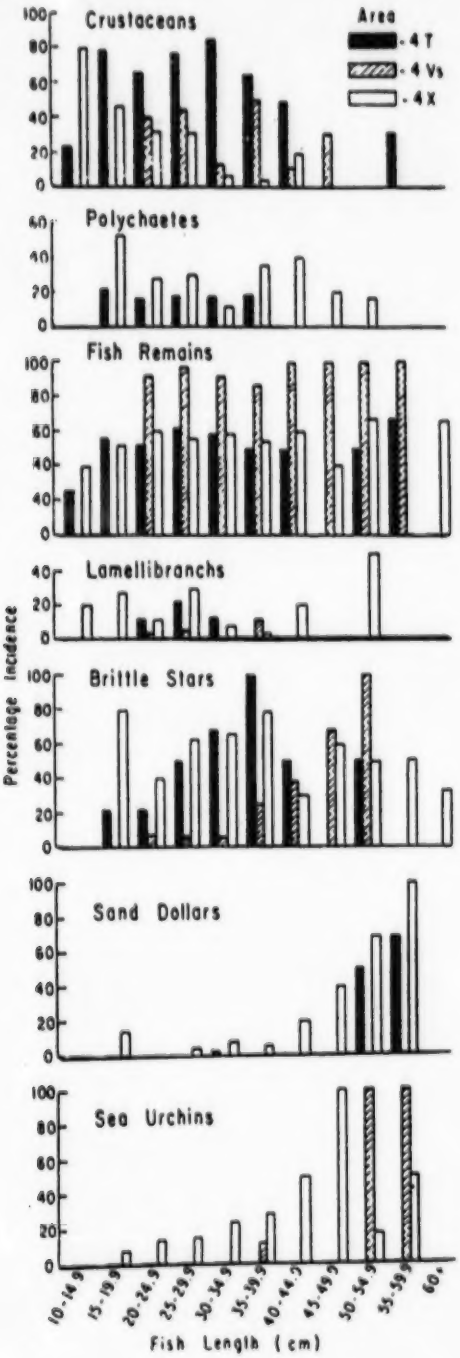
Fish species	Estimated absolute biomass (tonnes)	Fish species	Estimated absolute biomass (tonnes)
Blueback herring	Few 100's*	Cunner	Many
Alewife	Few 100's*	American sand lance	-
American shad	Few 100's*	American mackerel	Many*
Atlantic herring	Many*	Bluefin tuna	-
Atlantic salmon	50+*	Rock gunnel	-
Brook trout	-	Wrymouth	-
Capelin	<10	Daubed shanny	-
American smelt	100?	Snake blenny	8
American eel	50+	Radiated shanny	-
Atlantic saury	-	Ocean pout	279
Mummichog	40	Atlantic silverside	-
Northern pipefish	-	Atlantic sea raven	-
Fourspine stickleback	-	Grubby	-
Threespine stickleback	-	Longhorn sculpin	90+
Black-spotted stickleback	-	Shorthorn sculpin	90?
Fourbeard rockling	-	Alligator fish	0.2
Atlantic cod	225*	Lumpfish	-
Silver hake	-	Atlantic seasnail	-
Pollack	Few*	Windowpane	3
White hake	399*	Little skate	148
Witch flounder	241*	Winter skate	148
American plaice	5579*	Thorny skate	32*
Yellowtail flounder	36*?		
Smooth flounder	Few		
Winter flounder	3010		

*These species are, to varying extents, migratory. The biomasses given for them are seasonal maxima.

Appendix 4: Prey composition (percent by volume) of Atlantic cod in southwestern Gulf of St. Lawrence, collected on fall groundfish surveys, 1959-1973,1980, presented in Waiwood (1981).

	Year																
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1979	1980
Euphausiids																	
30	20.36	15.57	6.25	8.33	40.51	56.10	45.69	4.26	46.33	4.17	2.63	1.90	32.00	29.29	55.79	-	24.22
-45	21.10	14.82	7.70	10.80	24.46	40.81	34.36	20.55	23.17	6.24	6.14	6.48	36.80	28.84	38.69	-	10.31
-60	9.77	15.24	7.32	6.95	17.77	32.12	28.39	24.49	12.52	10.82	5.21	9.33	33.64	32.45	30.03	-	8.62
-75	6.46	3.05	1.90	6.74	7.46	18.13	16.89	11.61	8.94	8.40	6.40	3.85	20.27	15.96	17.65	-	7.67
75	0.22	1.43	5.88	2.86	1.39	3.43	15.56	0	0	0.57	4.08	0.85	0	1.59	0.24	-	1.03
Amphipods																	
30	31.09	20.57	26.70	44.54	8.52	15.93	11.57	49.79	20.33	28.75	1.45	15.57	4.00	9.52	1.58	-	3.89
-45	15.52	13.95	13.88	23.58	12.27	12.29	12.36	15.22	11.67	13.13	2.71	9.72	3.42	5.13	2.84	-	6.78
-60	10.92	12.24	10.20	12.32	12.02	7.69	3.05	5.57	9.32	5.14	2.76	5.94	4.23	3.62	1.09	-	3.80
-75	3.51	2.85	5.86	6.27	4.05	2.08	2.56	0.22	3.61	1.87	0	2.40	1.96	1.25	0	-	2.20
75	0	8.08	0	0.65	5.97	0	0	0.19	0	0	0	0.85	2.00	0	2.38	-	0.29
Mysids																	
30	6.97	35.10	26.70	8.44	21.02	4.32	0	0	0	23.42	44.87	35.06	0	0	0	-	0
-45	3.78	24.82	8.59	6.26	2.81	0.72	0	0	0	5.71	30.21	14.65	0	0	0	-	1.23
-60	2.15	9.19	5.78	2.46	1.84	0.21	0	0	1.23	1.74	18.01	8.09	0	15.00	0	-	0.75
-75	0	1.69	0	1.00	2.58	0	0	0	0	0.22	17.12	4.30	0	0	0	-	0.43
75	0	0	0.59	0.17	0	0	0	0	0	0.80	6.58	0.85	0	0	0	-	0.01
Decapods																	
30	24.38	14.73	18.75	13.91	9.38	7.97	7.84	11.17	4.00	3.33	15.00	12.00	32.00	9.52	23.58	-	18.89
-45	26.30	17.73	30.87	11.38	21.74	12.11	10.88	12.14	14.44	20.99	19.53	20.04	23.06	12.07	24.55	-	15.33
-60	21.69	17.76	21.96	17.35	26.72	13.75	20.31	15.12	21.60	24.58	24.85	19.95	13.24	14.27	25.17	-	13.85
-75	24.50	21.42	23.47	14.92	16.42	28.37	27.68	21.51	32.66	19.33	19.14	21.60	19.55	16.58	27.65	-	25.66
75	17.59	21.39	29.71	13.06	12.20	16.00	14.81	10.37	22.33	10.57	9.08	19.24	14.03	3.97	25.71	-	33.71
Molluscs																	
<30	0.41	0.72	0	1.85	2.27	1.35	1.96	1.06	0	0	0	0	0	0	1.05	-	7.45
1-45	6.62	3.91	11.60	10.80	2.51	7.69	8.55	6.54	1.98	2.70	0.55	7.25	4.87	7.84	6.38	-	15.48
6-60	12.40	10.64	20.92	19.40	8.11	17.62	10.59	8.44	6.75	7.51	3.07	13.60	9.70	15.51	12.00	-	25.91
1-75	15.91	6.67	12.22	12.57	4.12	16.49	10.12	7.53	6.60	4.40	2.30	10.70	12.52	12.47	14.01	-	19.27
>75	3.86	0.71	7.94	10.34	3.06	2.86	8.52	3.70	1.67	0.68	0.26	2.20	1.60	0.79	2.38	-	16.15
Annelids																	
<30	7.58	3.29	7.61	10.87	2.95	1.76	5.10	4.36	0	6.75	3.95	14.56	4.00	0	4.74	-	3.11
1-45	10.94	12.28	17.23	18.87	12.65	6.36	10.69	7.53	6.75	8.31	11.91	16.58	8.03	4.91	6.19	-	7.44
6-60	13.96	12.14	14.22	17.46	7.78	5.07	5.16	6.40	7.67	9.73	11.66	17.31	12.38	7.24	4.51	-	6.04
1-75	6.28	5.74	16.90	5.53	2.42	2.22	2.62	2.58	1.60	3.58	3.53	9.75	6.82	4.40	2.95	-	3.26
>75	5.47	0	5.29	3.08	3.06	0	0	5.56	1.00	0.80	0.39	3.73	1.80	3.17	2.38	-	3.30
Echinoderms																	
<30	0	0	0	0.23	0	0.68	0	1.06	0	0	0	0	4.00	0	5.79	-	0
1-45	1.41	1.11	2.43	2.21	2.03	4.73	2.25	3.08	0	0.48	0.85	1.90	2.12	3.45	3.47	-	0.43
6-60	4.82	3.67	5.29	5.10	7.80	5.93	2.31	3.24	0.61	1.37	0.37	4.70	3.43	3.47	2.69	-	3.03
1-75	5.35	3.40	8.43	6.21	35.99	4.31	1.83	3.66	5.21	2.39	0.72	6.30	2.71	3.13	5.53	-	3.23
>75	8.22	0	2.94	5.75	0.83	3.14	0	0	0	4.55	2.10	1.86	0.80	0.32	2.38	-	2.04
Other Invertebrates																	
<30	0	1.98	9.66	7.94	2.27	5.41	0	0	0	1.67	3.95	0	4.00	0	0	-	0
1-45	3.08	0.51	4.21	5.00	4.34	1.10	0.87	1.37	0	1.42	2.16	2.78	0.44	0.56	0	-	0.90
6-60	2.57	0.85	3.06	4.63	3.37	0.92	0.38	0.66	0.37	0.53	5.09	2.39	2.54	1.36	0.39	-	0.53
1-75	1.53	0.14	0.34	1.00	2.13	2.50	0.61	1.08	1.06	0.82	0.79	1.00	1.96	0.43	0.23	-	0.30
>75	2.22	7.14	0	0.85	3.89	0.57	1.85	0	0	0	2.63	0.08	0	0.16	0	-	0

Appendix 4 (con't)

Size category (cm)	1959	1960	1961	1962	1963	1964	1965	1966	Year 1967	1968	1969	1970	1971	1972	1973	1979	198(
Capelin																	
<30	0	0	0	0	0	0	0	0	0	7.50	0	0.63	4.00	0.48	0	-	0
31-45	0	0	0.18	0	1.18	1.14	5.97	8.90	8.49	20.80	2.54	1.23	9.82	3.84	0.75	0	0
46-60	0	0.60	0.53	0	0.35	2.17	12.47	17.09	8.47	19.93	4.54	1.32	8.70	3.25	2.72	4.90	0.(
61-75	0	0	0	0	0	0.83	1.22	11.72	5.11	19.10	0.86	0.25	3.00	0	6.36	4.67	0
>75	0	0	0	0	0	0	0	3.52	0	1.14	0.13	0	0	0	4.76	1[illegible].66	0
Herring																	
<30	0	0	0	0.18	0	0	0	0	0	0	0	0	0	0	0	-	0
31-45	0.68	0.72	0.16	0.91	0	0	0	0	0	0	0	0	0	0	0	0	0
46-60	1.92	4.08	4.54	4.17	0	0.68	0.31	0	0.86	0.68	0.46	1.08	0.96	0	0.87	0	0.1
61-75	9.24	22.22	19.14	22.83	2.77	0.69	7.32	10.75	1.06	7.46	14.46	13.95	9.44	3.74	2.27	0	0.9
>75	21.33	8.57	10.29	27.31	9.72	14.86	14.81	41.85	51.67	31.14	48.95	44.83	17.80	10.95	24.29	9.60	0
Flatfish																	
<30	0	0	0	0	0	0	0	1.06	0	0	0	0	4.00	4.76	0.53	-	14.8
31-45	0.50	1.26	0	0.13	0	0	0	0.55	0.40	0	0.34	1.44	1.54	1.42	0.56	-	1.1
46-60	1.61	2.22	0.24	0.85	0	0	0	0.82	2.45	0.62	0.37	1.29	2.06	1.33	2.21	-	1.2
61-75	3.45	3.82	2.76	1.58	0	0	0	0	2.77	0.97	3.17	4.70	4.18	5.65	1.21	-	5.1
>75	2.92	20.40	1.47	12.89	1.39	2.86	0	1.85	1.33	4.55	2.50	8.56	16.27	4.13	4.52	-	17.1
Gadoids																	
<30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0
31-45	0	0	0.07	0	0	0	0	0	0	0	0	0	0	0	0	-	0
46-60	0.38	0	0.48	0.17	0.55	0	0.31	0	0	0	0	0	0	0	0	-	0.1
61-75	1.45	1.39	0.86	0.48	0	0	0	0	1.06	0.37	0	0	0	0	0	-	0.5
>75	6.67	7.14	12.65	3.39	0	1.43	0	1.85	4.33	0.91	1.84	0	6.50	0.48	2.14	-	3.1
Mackerel																	
<30	0	0	0	0	0	0	0	0	0	0	0	0	0	2.38	0	-	0
31-45	0	0	0	0	0	0	0	0	0	0	0	0	0	0.43	5.00	0	0
46-60	0	0	0	0	0	0	0	0	0	0	0	0	0.70	3.62	5.13	0.87	0
61-75	0	0	0	0	0	0	0	0	0	0	0	0	0.93	3.48	5.91	0	0
>75	0	0	0	0	0	4.57	0	0	1.00	0	0	0	12.80	32.06	7.14	10.20	0
Other Fish																	
<30	3.46	0.57	0	0	0	0	0	1.06	0	0	4.61	3.80	0	3.57	2.11	-	0
31-45	2.32	1.46	1.25	0.52	1.12	1.59	2.12	0.82	1.19	0.31	1.78	1.73	0.83	3.62	3.99	-	1.46
46-60	1.88	1.42	1.00	1.63	0.39	0.24	1.09	1.07	4.05	1.32	3.68	2.50	1.89	2.01	2.89	-	1.40
61-75	1.73	3.23	0.86	2.58	0.53	1.39	1.83	1.51	10.85	1.46	2.73	1.95	3.55	4.17	4.47	-	1.55
>75	1.33	0.71	0	3.56	2.78	0	11.11	3.33	4.33	0.45	0	2.29	3.00	3.17	1.90	-	0
Unidentified fish																	
<30	2.54	0	0.91	0.34	0.57	1.35	0	0.85	3.33	3.58	2.63	2.53	4.00	4.76	3.79	-	0
31-45	4.66	0.96	1.01	1.13	4.84	8.58	7.19	7.64	13.49	6.80	6.23	5.07	4.11	13.84	6.08	-	5.57
46-60	10.43	3.05	2.88	1.58	7.01	11.15	10.75	11.52	11.66	8.50	7.85	8.90	4.41	8.14	9.55	-	5.73
61-75	17.54	12.49	5.53	7.62	9.47	19.10	20.98	20.75	10.21	16.23	9.57	12.40	7.29	26.07	11.74	-	15.92
>75	29.97	11.55	21.18	11.19	34.19	43.71	29.26	27.78	8.67	25.45	11.84	9.66	20.80	39.21	19.76	-	15.79
Miscellaneous Items																	
<30	0.09	8.17	0	3.09	12.50	5.14	27.84	10.96	26.00	20.00	19.61	12.66	4.00	35.71	1.05	-	26.50
31-45	1.46	4.97	0	6.44	10.15	1.89	4.75	10.44	17.62	12.63	14.32	10.42	4.39	14.05	1.49	-	33.77
46-60	4.29	3.80	0	4.84	5.96	2.17	4.22	4.63	12.27	6.78	10.40	3.20	1.93	3.25	0.39	-	27.55
61-75	2.28	9.82	0	9.09	12.07	3.89	5.85	5.38	5.32	12.84	17.34	5.95	4.58	2.67	0	-	13.83
>75	0.20	12.86	0.59	4.92	21.53	6.57	0	0	3.67	17.50	8.29	4.24	1.60	0	0	-	7.35
Sample Size																	
<30	109	84	85	353	80	74	51	94	30	120	76	79	25	42	95	-	22
31-45	234	462	274	1194	195	264	231	182	126	415	236	284	228	232	268	21	482
46-60	260	273	209	984	311	292	320	244	163	438	326	372	301	323	357	116	748
61-75	145	72	58	209	94	72	82	93	94	268	139	200	107	115	132	80	199
>75	45	14	34	59	36	35	27	54	30	88	76	118	50	63	42	23	46

Appendix 5: Percent incidence of food items in American plaice stomachs, by fish length and area (Scott, 1973).